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ANNIVERSARY ADDRESS

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AN ICHTHYOLOGIST LOOKS AT INDIAN PALAEOGEOGRAPHY.

Today, in India as elsewhere, we are once again inclining towards a unitary view of knowledge: indifferent specialization alone leads away from it. This fact is not just a suitable, perhaps provocative, introduction to an address such as this, for I have experienced its truth deeply in my work. In my principal subject, Ichthyology, for example, I have found that the more intensively I studied it, the more extensive my enquiries and approaches have become. I had to acquire perspectives from other sciences and kindly specialists in other disciplines; I had to find relevant patterns of thought in history and patterns of life in geology; and periodically I had to reassess what I had learned and relate it to the march of science in our country. Otherwise, there was no purpose in learning it.

On this anniversary occasion, I am encouraged to offer you another of these syntheses, my purpose this time being to consider some of the paleogeographical problems of India in the light of contemporary information about the evolution and distribution of our freshwater fishes. The major points I shall try to make are that the northern landmass and Gondwanaland were connected by a land bridge in the Assam region until the Middle Eocene; that the Himalayan foredeep of the Miocene-Pliocene period could not have been the Indo-brahm or Siwalik River of the geologists; and that the Garo-Rajmahal Gap became a physiographic feature of India only during the glacial epochs of the Pleistocene. I hope that certain other points will also emerge as I proceed.

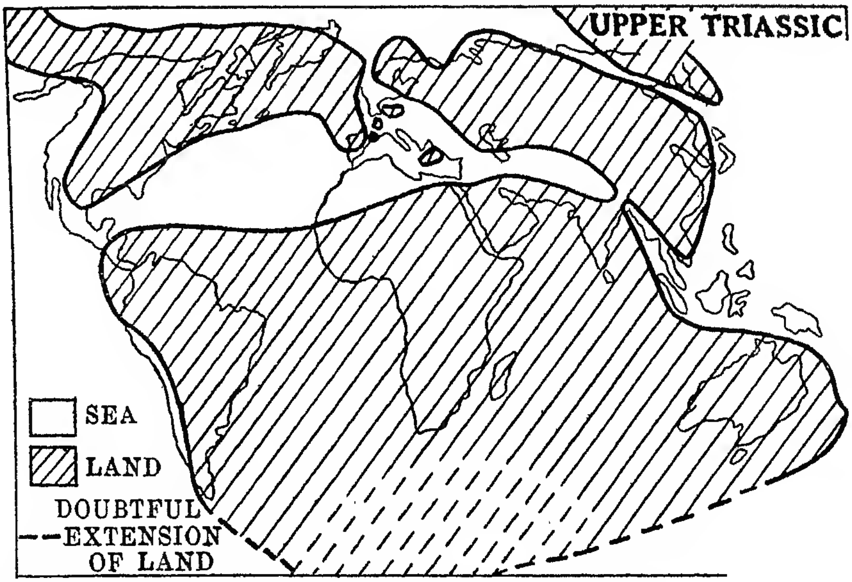
Freshwater Fishes of the Triassic.

Our earliest known freshwater fishes were Dipnoans or Double-Breathers, popularly known as 'Lung-Fishes'. It is characteristic of them that, in addition to having gills for aquatic respiration, their air-bladders are modified to function as lungs for aerial respiration. They have not survived in India, but we find their fossil remains in the Maleri Beds of the Godavari Valley, which are stated to be definitely of the Upper Triassic Period, about 170 million years ago. Their present-day discontinuous distribution in Australia, Africa and South America is further evidence of their great antiquity.

The Dipnoans are represented in the Indian fossil fauna by the genus *Ceratodus* Agassiz, which had evolved during the early Triassic in the northern landmass and soon became the dominant freshwater fish of the period. It is necessary at this stage to have an idea of the geography of the world during the Trias. There was then the Gondwanaland in the south, which, besides Peninsular India, included Australia, Madagascar, the southern parts of Africa, South America and Antartica; and a northern landmass in the north, which included North America, Europe, Siberia, China and Indo-China. These two continental units are believed to have been separated by an east-west running ocean called the Tethys, of which the Mediterranean Sea is now the remnant.

The migration of *Ceratodus* to the Gondwanaland shows that in the Lower Triassic a land bridge had been established, which divided the Tethys Ocean and made it possible for *Ceratodus* to spread all over the Gondwanaland. From India, it wandered to Australia in the Lower Triassic, and continued to live there until the Upper Cretaceous: its fossils are found in Africa from the Lower Triassic to the

Upper Cretaceous, but in South America its fossils are known only from the Upper Cretaceous beds.



TEXT-FIG. 1. The northern landmass and Gondwana during the Trias. Modified after Dr. A. C. Seward (*Plant life through ages*, 1931).

The genus is now extinct, but a very closely allied form, *Epiceratodus* Teller, is now found in Queensland. During my visit to Australia in 1951, I had several opportunities of seeing this fish and, not finding it coming to the surface, I was surprised to learn that in well-aerated aquaria or ponds, the fish never comes to the surface to breathe. Aerial respiration is resorted to only when the water becomes foul and deficient in oxygen. It has already been recorded by Bridge (1904, p. 510) and Romer (1947, p. 123) that this fish is not capable of burrowing in mud, like the Dipnoan fishes of Africa and South America to which we shall refer presently.

Ceratodus and Climate.

The distribution of *Ceratodus* in space and time, and its ecology as inferred from the habits of *Epiceratodus*, gives us some clue to the climates of the Triassic Period. There were large rivers, which often flooded the neighbouring areas and filled up extensive perennial depressions. The vegetation, which was carried by floods in the same depressions, was still fairly luxuriant. There must have been dry periods of prolonged duration when the vegetation decomposed and used up dissolved oxygen. These were evidently unfavourable conditions for fishes, but *Ceratodus* could survive them.

In North America, Europe, Africa and Australia, the dry seasons seem to have lasted for longer periods, thus bringing about the fossilization of *Ceratodus* from the Lower Triassic period. India experienced complete desiccation in the Upper Triassic, when the Dipnoan fishes perished; but favourable conditions for their existence seem to have persisted in other areas until the Upper Cretaceous period. In Queensland, the ecological conditions of the Lower Triassic seem to have continued, more or less unchanged, to the present time, with the result that *Ceratodus* has come to us almost in the same form as *Epiceratodus* in that part of the world.

In Africa, *Ceratodus* seems to have given rise to *Protopterus* Owen under long-persisting marshy conditions, lasting over millions of years, which probably induced the habit of burrowing in mud and thereby tiding over conditions of drought. This habit led to elongation of the form, degeneration of paired fins, reduction of scales, and so on. In South America, these tendencies seem to have been still further accentuated with the result that *Lepidosiren* Fitzinger is more or less an eel-like fish, capable of aestivating in its underground cocoon for very long periods. That such has been the course of events is further illustrated by the modifications undergone by fishes of the Magur family (Clariidae: Siluroidea) on their arrival in Africa from India during the Pliocene period, at the most about 10 million years ago.

Freshwater Fishes of the Jurassic.

After a period of desiccation during the Upper Triassic, the conditions seem to have become favourable again during the later Triassic; for we find that the Gondwanaland received an invasion of the Ganoid fishes from the north about the end of the Upper Triassic or beginning of the Lower Jurassic period. Australia appears to have separated from the Gondwanaland at this time, since, no Ganoid fish seems to have migrated to Australia. The shrunken Gondwanaland comprised Peninsular India, Madagascar, South Africa and South America.

The remains of the Ganoid genera *Lepidotus* Agassiz, *Tetragonolepis* Brown and *Depedius* Leach are found in the Upper Jurassic Kota Beds of the Godavari Valley. Of these, *Lepidotus* seems to have arrived earlier, for it spread to Madagascar and South America. All the three genera are extinct at present, having died out in the Upper Jurassic. In Madagascar, they became extinct in the Lower Jurassic, while in South America they persisted till the Lower Cretaceous.

Freshwater Fishes of the Cretaceous.

By the Lower Cretaceous, favourable ecological conditions for fish life seem to have been established again, when another invasion of Ganoid fishes (*Pycnodus* Agassiz, and *Lepidosteus* Lacépède) took place. *Pycnodus* is extinct at present, but its fossils are known from North America (Lower to Upper Cretaceous), Europe (Lower Cretaceous to Eocene), India (Upper Cretaceous) and Africa (Eocene). *Lepidosteus* appeared somewhat later and is still living in Eastern North America, Central America and Cuba. Its invasion of the Gondwanaland extended only as far as India.

Both these genera became extinct in India with the earliest phase of the lava eruptions that formed the Deccan Traps. Their fossils are found in the Upper Cretaceous Lameta Beds at Dongargaon. In my opinion, these fishes did not survive long in India and Africa to spread to South America, because some later records of fish distribution show that South America still formed a part of the Gondwanaland during the Upper Cretaceous. Their fossil records from India show that trap formation in the Deccan commenced in the Upper Cretaceous, and brought about a vast devastation of the fauna and flora.

Freshwater Fishes of the Eocene.

After the first phase of the extensive lava flow had ended, normal conditions gradually returned again; and another invasion of the Ganoid fishes of the genus *Lepidosteus* took place early in the Eocene, about 60 million years ago. They provide evidence that the Assam land bridge was still in existence, and that Africa and India still formed a part of the truncated Gondwanaland. Another phase of volcanic eruption exterminated the last known Indian Ganoid fishes, their fossil remains from the Inter-trappean beds at Paharsingha and Kateru being described by myself in 1938.

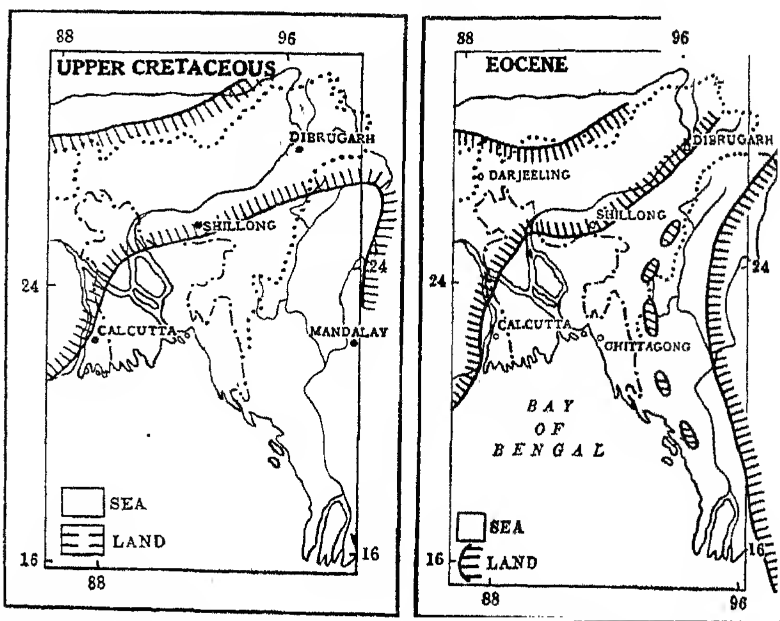
About the same time, some Teleostean fishes also invaded the Gondwanaland from the north. Representatives of one remarkable family, the Osteoglossidae, were described from the Inter-trappean beds of Deothan (Hora, 1938). The now extinct genus *Musperia* Sanders is not only recorded from India, but from the Upper Eocene beds of Sumatra as well; and it is further remarkable that the modern genus *Scleropages* Günther, an undoubted descendant of *Musperia*, is now found in Thailand, the Indo-Australian Archipelago and Australia.

The palaeogeographic conclusion is that the mainland of Asia at that time was directly connected with Australia, through Sumatra and other islands of the Malay Archipelago. Thus, after its severance from the Gondwanaland, Australia became directly connected with the northern landmass, but this connection seems to have lasted only for a short period; for the Acanthopterygian fishes that spread to Africa and South America on the one hand, and to the Indo-Australian Archipelago on the other, do not seem to have reached Australia.

The varieties of Acanthopterygian fishes known from their fossil scales, embedded in the Inter-trappean beds at Deothan, Kheri and Takli, indicate that they lived in marshy, estuarine conditions. Some variety of *Koi Machch* (*Polycanthus* C.V.), and allied fishes of the family Nandidae (*Nandus* C.V., and *Pristolepis* Jerdon), formed the bulk of the fish-fauna of that period, which not only spread over the whole of South-East Asia but also entered Africa and South America. Like the Dipnoan and Osteoglossid fishes, the discontinuous distribution of the families Nandidae and Anabantidae shows their great antiquity.

Absence of Freshwater Fishes in the Miocene.

Though carps and catfishes dominate the freshwater fish-fauna of India today, and though they had made their appearance on the mainland of Asia during early Eocene times, the conditions over the Assam land bridge do not seem to have been



TEXT-FIG. 2. Transgression of the Bay of Bengal during the Eocene. For comparison a map of the Cretaceous period is also given. Modified after Dr. M. S. Krishnan (*Bull. Nat. Inst. Sci. India*, 1, pp. 25–26, 1902).

favourable for their migration to India. One fragment (a scale) was doubtfully referred by me (1938, p. 274) to the Ambramidinae, which includes very primitive varieties of the carp family. Some primitive genera of Indian carps are found in Africa too, which adds weight to the probability that the early Eocene fish-fauna of India included *Musperia, Polycanthus, Nandus, Pristolepis* and *Rasbora*; but the eruption of the Deccan Traps during the Lower Eocene seems to have exterminated them completely.

During the Middle Eocene, a transgression of the Bay of Bengal northwards snapped the Assam land bridge and separated India from the rest of Asia. The transgression of the sea also made it impossible for freshwater fishes to invade India. The dating of the period of this transgression has been made possible by Sri A. G. K. Menon's recent identification (seen in MS.) of a marine Pycnodont Ganoid fish from the Middle Eocene marine deposits of the Garo Hills in Assam.

With the breaking up of the Assam land bridge, freshwater fishes could no longer invade India, while those that had crossed over in the Lower Eocene were exterminated by the successive outbursts of lava. Consequently, there was no freshwater fish in India throughout the Miocene period. This surmise is supported by the absence of freshwater fish in the Indian deposits of this period.

Freshwater Fishes of the Pliocene.

The next invasion of freshwater fishes from China to India took place in the Pliocene, as we know from the Siwalik fossils. The earliest fossils are those of the Siluroid (*Nagur*) genera *Clarias* Scopoli and *Heterobranchus* Geoffroy. They are specialized air-breathing fishes, which flourish in marshy areas and are capable of tolerating very low salinity. The remains of an Acanthopterian air-breathing fish, *Ophicephalus* Bloch, are also known from the Siwalik deposits, it being presumed that this fish wandered to India along with *Clarias* and *Heterobranchus*. In the Pliocene Siwalik beds, probably of a somewhat later period, are remains of other sluggish-water catfishes of the genera *Chrysichthys* Bleeker, *Mystus* Scopoli and *Rita* Bleeker. Somewhat later still, two other genera of Siluroid fishes, *Bagarius* Bleeker and *Silurus* Linnaeus, probably migrated to India, their remains being entombed in the Siwalik rocks. These fishes live in clear waters at the bases of hills.

The freshwater fishes of the Siwalik period enumerated above fall into three ecological associations:

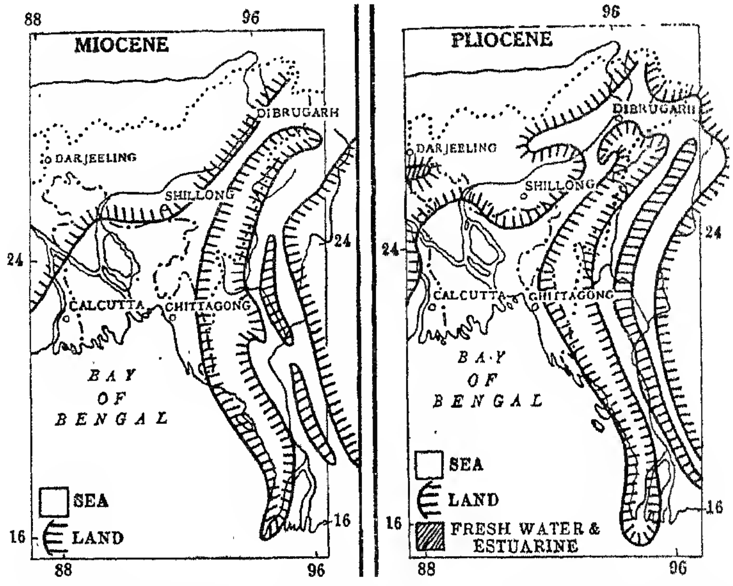
(1) Air-breathing fishes of marshy areas: *Clarias, Heterobranchus* and *Ophicephalus*.
(2) Fishes of pools, ditches and other sluggish-water areas: *Chrysichthys, Mystus* and *Rita*.
(3) Fishes of clear, flowing waters: *Bagarius* and *Silurus*.

It is presumed that the clear water fishes were the last to arrive in India for the following palaeogeographical reasons.

We have noticed that the Bay of Bengal extended northwards to China and Tibet from the Middle Eocene, and that the sea very probably separated India from the rest of Asia during the whole of the Miocene. At the close of the Miocene, or early in the Pliocene, the sea would seem to have receded southwards, leaving stretches of low marshy areas extending between China and India. As most of the monsoon winds of that period must have crossed to the north over this marshy area, it can safely be presumed that its ecological conditions during the early Pliocene must have been similar to those of Lower Bengal at the present time.

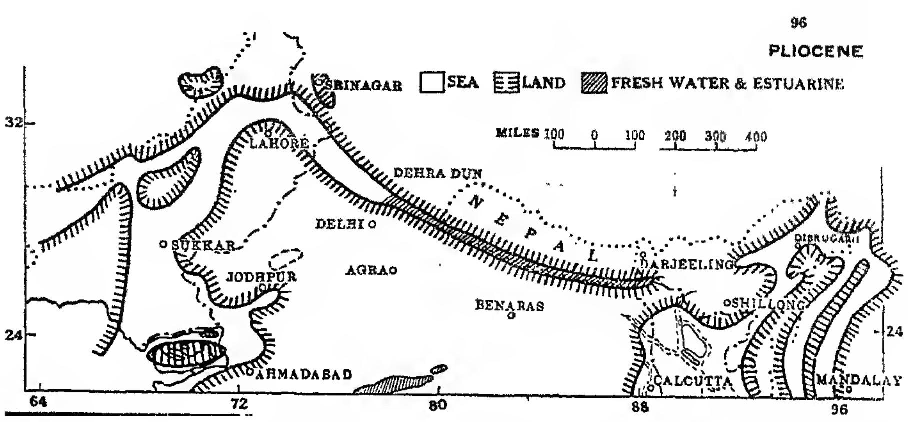
It was under such conditions that the air-breathing fishes populated this region and spread to India. In fact, *Clarias, Heterobranchus* and *Ophicephalus* were able to cross the whole of India and the Middle East to spread as far as Africa. There is

abundant evidence from the Siwalik fossils that marshy conditions dominated the early Pliocene along the southern foot of the Himalayas. Gradually, marshy



TEXT-FIG. 3. Distribution of land and sea in the Bengal, Assam and Burma regions during the Miocene and Pliocene periods. Modified after Dr. M. S. Krishnan (*Bull. Nat. Inst. Sci. India,* 1, pp. 27-28, 1902).

conditions were replaced by drier lands, with pools and ditches, which gave India *Chrysichthus*, *Mystus* and *Rita*. Towards the end of the Pliocene, the low east-westwards hills of the young Himalayas seem to have made their appearance in the region between China and India, thus making the westward dispersal of *Bagarius* and *Silurus* possible. Therefore, during the Pliocene there were three invasions of

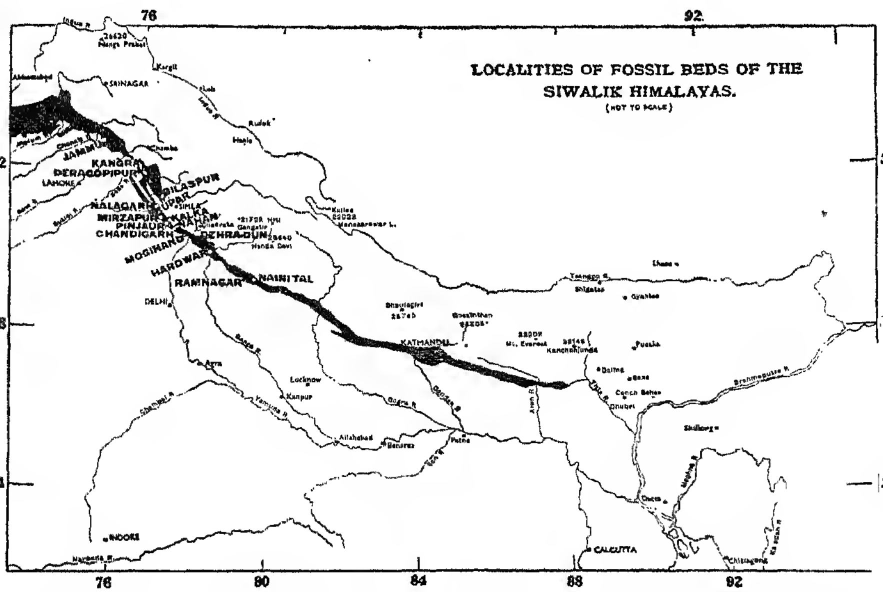


TEXT-FIG. 4. The Siwalik foredeep of the Pliocene period. Modified after Dr. M. S. Krishnan (*Bull. Nat. Inst. Sci. India,* 1, p. 28, 1902).

freshwater fishes, but they only spread along the base of the young Himal in the continuous foredeep. They did not move down into Peninsular India.

THE SIWALIK FOREDEEP.

The location of all the Siwalik freshwater fish fossils between a narrow stretch of the hills between Naini Tal and Jammu raises several points of interest in palaeogeography; and one is almost forced to join in the controversy about the existence or non-existence of an Indo-brahm or Siwalik River at the base of the young Himalayas. Much has been written on this subject without achieving unanimity, so that a zoologist can be forgiven for taking it for granted that the relevant geological evidence is ambiguous. I shall attempt a solution on the evidence of fish distribution.



TEXT-FIG. 5. Northern India showing the Siwalik rock and the fossiliferous beds (indicated by white dots) so far known (after A. G. K. Menon in MS.).

The location of the Siwalik freshwater fish fossil beds between Ramnagar (near Naini Tal) in the east and Jammu in the west indicates that, in the Siwalik foredeep, a calm zone for sedimentation existed in this region. In fact, Dr. M. S. Krishnan's recent palaeogeographical map, in his contribution to the Rajaputana Desert Symposium, published in the first Number of the *Bulletin of the National Institute of Sciences of India*, may be interpreted as showing that the tidal salt water from the west and fresh water from the east mingled in this area, thus producing a dead water zone with no appreciable currents from any direction. Now the question is, when was the foredeep produced? And the answer is that on the fossil evidence it was in existence in the Lower Pliocene. But its earlier existence is not ruled out, for the transgression of the Bay of Bengal since the Middle Eocene permitted no freshwater fauna which could yield fossil evidence for the Miocene epoch.

Geologists tell us that the most violent compressive movements occurred about the Middle or Upper Miocene, when the whole of the marine basin, now the seat of

the Himalayas, was raised up into dry land. According to Dr. M. S. Krishnan (1952), 'the compression had also the effect of forming a depression along the front (south) of the Himalayas. This was a long narrow furrow, or a series of furrows, stretching from the north-east corner of India all along the front of Himalaya to Jammu and Potwar Plateau and thence down south to the west of the Indus valley.' From the physiography of the country during the Miocene, it can be reasonably inferred that the greater part of the drainage of northern India was from east to west; and that the furrow referred to above helped to carry the drainage to the west into the sea, even though there was no significant gradient, since the sea then extended over the Assam region as well. 'As compression advanced', says Dr. Krishnan, 'and the mountains in the north steadily increased in height, the shallow depression (technically called the foredeep) at the front became deeper and deeper.' It is thus clear that the foredeep was formed in the Middle Miocene, since the mid-Miocene orogeny was the most violent of all the Himalayan movements.

Numerous streams must have drained into the furrow from the newly formed mountains. During the Murree period (Oligocene—Lower Miocene), the waters in the furrow in the north-west Punjab were brackish, but they gradually reached freshness by the mid-Miocene. There is evidence in the Punjab Himalayas (from the presence of the Murree sandstones) that a furrow may have come into being even in the Oligocene. There are no Murree sediments in the East Punjab and U.P. Himalayas, but the Dagshai and Kasauli beds in the Simla Himalayas seem to have been formed in lagoons.

Upper Tertiary Geography: The Pliocene Furrow.

Before proceeding further, let us visualize the geography of northern India at about the close of the Miocene and the commencement of the Pliocene. There was a chain of low hills in the north, with a continuous narrow furrow to the south of them. The Bay of Bengal had receded from the Assam Himalayan region, and marshy areas had been formed in the regions from which the sea had receded. The migration of fishes from east to west shows that even these marshes drained into the furrow.

Thus, though there was no actual river flowing from Assam to the Arabian Sea, there was a furrow that provided westward drainage for the whole of northern India. The waters in this furrow were brackish and tidal as far as Jammu; they were calm and dead as far as Naini Tal; thereafter, to the east, they were fresh and presumably flowing from east to west. Throughout the Pliocene, this furrow formed the repository of everything washed down from the land and the young Himalayas, and these sediments ultimately gave us the Siwalik Hills.

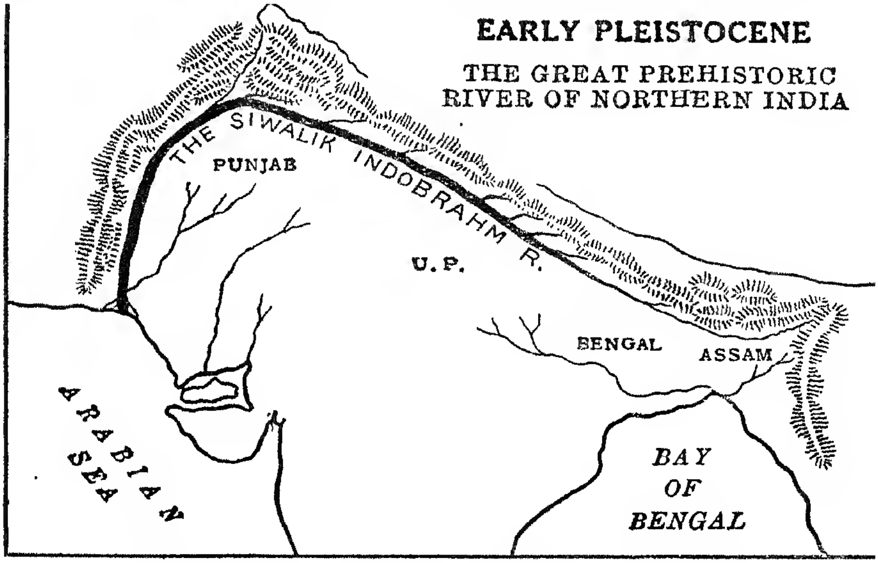
Let us now follow up the events after the formation of the Siwalik Hills in the late Pliocene.

The Pleistocene Foredeep.

Dr. Krishnan (1952, p. 46) tells us that, after the Middle or Upper Miocene phase of compression, 'the next two phases of the compression occurred at the end of the Pliocene period and during the Pleistocene to Sub-Recent period. The Pleistocene movement was particularly intense in the north-western Himalayas, as they brought about the rise of the Pir Panjal Range.' Dr. D. N. Wadia (1952, p. 14) is also emphatic on this point, for he says that 'It is a well-documented fact that the Himalaya Mountains have been elevated more than five thousand feet since the coming of Man on earth, itself the last great event in our Planet's history'.

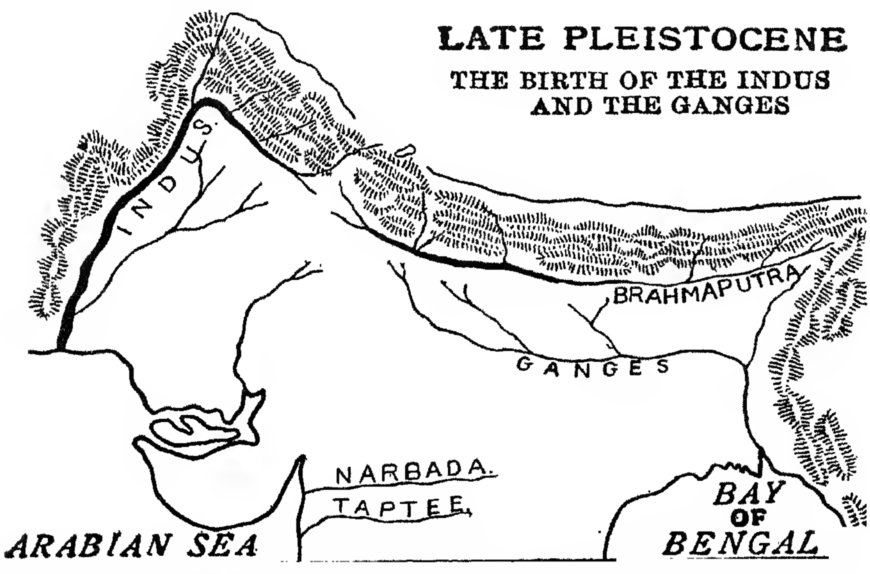
The result of the compression movement of the late Pliocene, and the subsequent Pleistocene movements, raised up the Siwalik sediments into dry land; and the foredeep gradually disappeared, leaving a shallow depression in which we find the Indo-Ganges-Brahmaputra Valleys of the present day. The foredeep

apparently moved southward, as the shallowing process went on leaving a narrow furrow at the base of the Siwaliks. This new foredeep, which for convenience we



TEXT-FIG. 6. The Pleistocene Indo-brahm River. After Dr. D. N. Wadia (*Proc. Nat. Inst. Sci. India*, 4, p. 389, 1938).

can call the Pleistocene Foredeep, must have taken up the function of draining northern India to the Arabian Sea.



TEXT-FIG. 7. The dismemberment of the Pleistocene Indo-brahm River. (After Dr. D. N. Wadia, *Proc. Nat. Inst. Sci. India*, 4, p. 389, 1938.)

By this time, the Assam plateau had come into existence, and so the foredeep could flow as a river from east to west: its remnant is the Indo-Gangetic Plain of our contemporary geography. In some places, the alluvium is surmised to be as deep as 18,000 feet, and below the alluvium the rock probably has the consistency of the rocks of the Siwalik Hills.

Thus, it would appear that a part of the Pliocene Foredeep also became a part of the Pleistocene Foredeep. Early in the Pleistocene, but not the Pliocene, we had an Indo-brahm River, which played a great part in bringing about uniformity in the Indo-Gangetic fish fauna; for it was during the Pleistocene that the greater part of the recent freshwater fish fauna of India entered the country. The present-day drainage of northern India resulted from the last phase of compression, which occurred in the Sub-Recent period.

Therefore, the dismemberment of the Indo-brahm took place in the very late Pleistocene, but before the fourth and fifth phases of glaciation, as is evident from the spreading of the Gangetic fauna to the Mahanadi and Godavari Rivers only when the sea-level was much lower than it is at present. This dismemberment enabled the Ganges and the Brahmaputra to find easy access to the sea through the Garo-Rajmahal Gap, which would appear to have been in existence before that period.

The Gap is so important a feature of the physiography of India from the view-point of fish distribution, that I shall now turn to discussing it.

THE GARO-RAJMAHAL GAP.

When the idea that the Vindhya-Satpura trend of mountains served as the main route of migration for the torrential fishes occurred to me in 1937, the Garo-Rajmahal Gap assumed special importance for biogeographical studies. Later, much evidence in favour of the Satpura Hypothesis of dispersal became available, and I (1944) provoked a discussion by writing an article on the probable age of the Gap. Several geologists took part in the discussion, but the position remained ambiguous. In 1949, in the Symposium on the Satpura Hypothesis, the Gap received considerable attention, but there remained the same ambiguity.

Other ecological factors have since been found (Hora, 1951) that permitted transgap dispersal of torrential animals, but the fact remains that the Gap seems to have acted as a barrier to fish dispersal during certain periods. Its chronology and physiography are accordingly of vital importance in the study of freshwater fish distribution in India. Therefore, we are greatly indebted to Dr. M. S. Krishnan (1952, p. 47) for clarifying the sequence of events which led to the formation of the Gap. He writes:

> 'In the early part of the Tertiary era, the Assam plateau did not exist and the area now occupied by it was under the sea, for we find strata of Eocene age along the southern margin of the plateau. The plateau seems to have been uplifted to the present position in the Miocene period. There is also some evidence that a series of uplifts took place in Chota Nagpur plateau during the Tertiary era. It seems likely that some weakness developed in the region between the Rajmahal hills and the Garo hills during the period of uplift of the Assam plateau, for we know that the northern margin of the plateau is marked by a rift or fracture (called a 'fault' by geologists), while the southern margin is a steeply dipping arm of a flexure or fold which plunges down into the Surma Valley. The Garo-Rajmahal gap may therefore have been formed either during the Miocene period of compression or later.'

According to Dr. Krishnan's maps of the land and sea boundaries of India during certain geological epochs, it would appear that the Assam plateau began to

make its appearance in the Miocene; for during that period the land and sea boundary in the region of Shillong would appear to be more or less the same as during the Eocene. The fault that produced the Gap may have occurred when the area was covered by the sea, for even the Pliocene map of Dr. Krishnan still shows it under the sea. As we have no fossil evidence of any fish dispersal to Peninsular India during the Pliocene, Dr. Krishnan's map must be regarded as correctly representing the land and sea boundaries over this region.

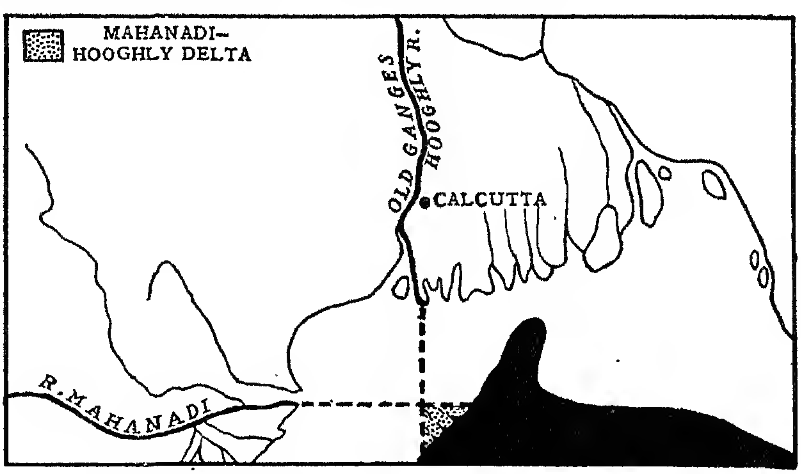
It should be added that, though the actual fault may have been either of Miocene or Pliocene age, the Garo-Rajmahal Gap seems to have taken its present form as a physiographic feature of India during the Pleistocene. It was only during the late Pleistocene that the Ganges and the Brahmaputra river-systems appeared as we know them today, and found their way to the sea through the Gap.

I have tried to show how, with the formation of the Himalayas and the Pleistocene Foredeep, freshwater fishes from the north-east colonized northern India. We shall now see how, with the Garo-Rajmahal area becoming dry land, the movements of fishes from the north-east were facilitated to Peninsular India. In any case, the present-day freshwater fish fauna of the Peninsula is not older than the Pleistocene.

Freshwater Fishes of the Peninsula Today.

We have seen that so long as the Assam land bridge between India and south-west China was in existence, Peninsular India was invaded several times by freshwater fishes from the north-east: Dipnoans during the Triassic; Ganoids during the Jurassic and Cretaceous; and Ganoids and Teleosteans during the Eocene. The fishes of the first two invasions died out completely owing to desiccation, while those of the later invasions were completely annihilated by the formation of the Deccan Traps. Moreover, with the breaking up of the Assam land bridge by the transgression of the Bay of Bengal during the Middle Eocene, no more freshwater fishes seem to have invaded this part of India until the Pleistocene period. There are no fossil records of freshwater fishes from Peninsular India after the Lower Eocene.

We have also seen that, with the formation of the young Himalayas, northern India began to receive freshwater fishes from China during the Pliocene. Their



Text-fig. 8. The lower courses of the Ganges and the Mahanadi during the height of a Glacial period (Hypothetical).

fossils in the Siwalik beds provide ample testimony to this effect. Peninsular India, on the other hand, received its fish fauna after the area covered by the Garo-Rajmahal Gap had become dry land during the Pleistocene. The periodicity of migration across the Gap was determined by the eustatic movements of the sea during the glacial epochs.

After the dismemberment of the Indo-brahm during the last glaciations, when the sea-level was a few hundred feet lower than it is now, the waters of the Ganges and Mahanadi probably formed a common delta permitting the mingling of the fauna. The fauna that had migrated to the Western Ghats along the Satpura trend of mountains, during the successive glacial periods, had the opportunity of spreading eastwards, and to the north of the Vindhya-Satpuras, when the tilting of the Peninsula occurred during the late Pleistocene.

All these aspects have been studied recently by my colleagues and myself (Hora, 1951; Menon, 1951; Silas, 1952; Hora, 1952, *in press*), and those who are interested in the Pleistocene geography of India should, I believe, find information of some value in these contributions. We have established, on the evidence of fish distribution and speciation through isolation and the dynamics of environmental changes, that the following geographical phenomena took place during the Pleistocene:

(1) The Garo-Rajmahal Gap appeared as a physiographic feature of India in the Pleistocene, as a result of the Pliocene-Pleistocene phase of compression of the Himalayas; or it may have appeared as dry land during the earlier glacial periods of the Pleistocene.

(2) In the foredeep of the rising Himalayas, there flowed a freshwater Pleistocene river, the Indo-brahm, from Assam to the Arabian Sea.

(3) Through eustatic movements of the sea during the glaciation phases, movements of fishes could take place across the Garo-Rajmahal Gap; and it is probable that freshwater fishes migrated to Peninsular India only during these favourable phases.

(4) The tilting of the Peninsula occurred during the late Pleistocene, and it was only then that its present-day west to east drainage was established. Before the tilt, there was an east to west Narbada-Tapti River, flowing at the base of the Satpura, into which drained the Mahanadi and the Godavari Rivers flowing north-westwards.

(5) During the last glacial phases, after the tilt and the dismemberment of the Pleistocene Indo-brahm, both of which may be the results of identical forces, the Ganges and the Mahanadi formed a common delta. Some contemporary tributaries of the Godavari may then have drained into the Mahanadi.

These are our principal conclusions. We feel they are of some importance to the development of Asian biology, and I have hoped to show in this address that geologists and geographers can use them as indicators for a fuller understanding of the palaeogeography of our country. Moreover, as I hinted to begin with, there is a larger purpose—perhaps you can call it a philosophical purpose—behind the correlative ideas I have had the honour of placing before you. It is the purpose of closer liaison between those of us who seem to be working at very different branches of knowledge, but whose results merge into a unity. Sometimes we are inclined to lose sight of this unity, to think that specialization is a narrowing down of one's interests rather than a means of enlarging the unity of knowledge by intensive studies; and if what I have said this afternoon, and elsewhere, helps to bring about a reorientation of scientific approaches in India I shall feel amply rewarded. The patience with which you have listened to me suggests that this point of view appeals to you, and I thank you very sincerely for your encouragement.

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Distribution of Himalayan Fishes and its bearing on certain Palaeogeographical problems.

By

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DISTRIBUTION OF HIMALAYAN FISHES AND ITS BEARING ON CERTAIN PALAEOGEOGRAPHICAL PROBLEMS.

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The physical and biological factors that govern the life of a torrential fauna[1] are of a very special nature and tend to restrict the distribution of hill-stream animals. Of the various physical factors, two are of special significance, the rapidity of the current and the consequent high percentage of dissolved air in mountain brooks. In response to the former, the organisms have developed various types of adhesive devices to prevent being washed away by the strong currents and spend most of their life clinging to rocks and boulders, while the greatly flattened or torpedo-shaped body presents a stream-lined form to the rushing current. As an adaptation to the high percentage of oxygen in these waters, the respiratory organs are reduced, for in such habitats even a comparatively much smaller area is sufficient to absorb enough oxygen for the requirements of an organism. Hill-stream animals are, as a rule, not suited for existence in muddy, sluggish water, and under such conditions usually die through asphyxiation within a very short period. As an example of biological factors, attention may be directed to the fact that the majority of the hill-stream fishes feed by scraping off algal slime and insect larvae that encrust rocks and stones, and consequently their mouths and jaws are specially modified for this purpose. It is obvious that the same method of feeding cannot be employed on a muddy substratum.

The distribution of the highly specialised hill-stream fishes, therefore, cannot be affected by the ordinary methods of dispersal along water channels, because the nature of the substratum[2] and the rapidity of the current are very potent factors for the existence of these animals. Their distribution along a mountain range has to be explained in terms of river-captures, longitudinal river valleys or tilting of mountain blocks so that the courses of the streams may alter without impairing their torrential nature. The distribution of the southern Himalayan fishes shows that all the three processes have been responsible in varying degrees for the dispersal of the fish fauna in this region, and that the Himalayan uplifting movement, though it may have been fairly uniform in the beginning over large areas, certainly became localised towards the end. Through the influence of these unequal orogenic movements, extending from the middle Eocene to almost within, geologically speaking, recent times, the Himalayas became hydrographically divided into a number of units which can be roughly demarcated with the help of their fish faunas. It is the object of this article to elucidate the probable

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[1] Hora, S. L.—Ecology, Bionomics and Evolution of the Torrential Fauna, with special reference to the organs of attachment. *Phil. Trans. Roy. Soc. London*, B, CCXVIII, pp. 171-282 (1930).

[2] Hora, S. L.—Nature of Substratum as an important factor in the ecology of Torrential Fauna. *Proc. Nat. Inst. Sci. India*, II, pp. 45-47 (1936).

boundaries of these hydrographical divisions of the Himalayas. Evidence is also adduced from the nature of the fish faunas of the north and south faces of the Himalayas to discuss whether the present-day drainage of the Himalayas is evolved from an ordinary " consequent drainage ", *i.e.*, the rivers flowed north or south of the crest, or is the result of an " antecedent drainage ". Observations are also made regarding the existence of the so-called " Indobrahm " or the " Siwalik River " of the Tertiary period.

DISTRIBUTION OF FISHES ALONG THE SOUTHERN FACE OF THE HIMALAYAS.

Ecologically, the Himalayan fishes can be divided into several categories and in discussing their geographical distribution it is well to bear in mind their respective associations. For instance, several species of *Barbus* Cuvier and *Labeo* Cuvier occur all along the Himalayas, but essentially they are forms of the plains which live in pools or deeper portions of the streams of the Himalayan foot-hills; some of them maintain themselves in swift currents through sheer muscular efforts. *Oreinus* McClelland, on the other hand, represents the Central Asiatic element on the southern face of the Himalayas; it spreads from Afghanistan, along the whole of the Himalayas and the contiguous ranges of hills, to south-eastern China. So far as is known, the fishes of this genus appear to be strictly residents of rivers in hilly regions, neither descending far into the plains nor occurring on level plateaux on the summits of mountains. Unlike the other Schizothoracinae, their mouths are provided with an adhesive device which enables them to resist being washed away in mountain torrents. *Oreinus* is a trout-like muscular fish and seems to have evolved from stocks of *Schizothorax* Heckel that may have been washed down from the Trans-Himalayan sections of some of our modern rivers.

A group of genera,[1] comprising *Crossochilus* van Hass., *Semiplotus* Bleeker, *Chaca* Gray, *Sisor* Hamilton, *Leiocassis* Bleeker, *Gagata* Bleeker, *Nangra* Day, *Bagarius* Bleeker, etc., is found in the streams of the foot-hills in comparatively deeper and less rapid-flowing waters; while Loaches or Loach-like cat-fishes, such as *Nemachilus* van Hass., *Lepidocephalichthys* Bleeker, *Acanthophthalmus* van Hass., *Somileptes* Swainson, *Acanthopsis* van Hass., *Olyra* McClelland, *Amblyceps* Blyth, *Erethistes* Müll. and Trosch., *Parasilurus* Bleeker, etc., live among pebbles and stones at the bottom and escape the effect of the rushing current. Though *Garra* Hamilton and *Glyptothorax* Blyth are provided with adhesive devices they are found both in torrential streams and in streams with moderate currents. These are essentially rapid-water forms, but have taken secondarily to slow waters. The typical torrential genera are *Pseudecheneis* Blyth, *Exostoma* Blyth, *Euchiloglanis* Regan, *Balitora* Gray and certain species of *Psilorhynchus* McClelland; these are res-

[1] Attention may also be directed to the amphibious, marsh-loving fishes of the genus *Ophicephalus* which are sometimes found at the sides of mountain streams in burrows and are not affected by the strength of the current. These are found throughout the plains of south-eastern Asia and are capable of wriggling about on wet ground.

tricted in their distribution to very fast flowing waters, and are accordingly the most highly adapted forms for life in mountain brooks.

Before discussing the distribution of the genera enumerated above, it seems worth while to form some conception of the age and geographical divisions of the Himalayas. According to Burrard, Hayden and Heron (p. 86)[1],

"Though the whole length of the great Himālaya range belongs to one geological age, yet the Punjab Himālaya are supposed to have arisen at a somewhat later date than the Nepāl Himālaya. The presence at elevations of 16,000 feet in the Punjab Himālaya of nummulites indicates that this portion of the range did not emerge from the sea till comparatively recently."

It is further stated that

"The rocks of the Siwalik range are stratified and date from the later half of the Tertiary period; those of the outer Himālaya are stratified also but are very much older."

For descriptive purposes the total length of the Himalayas from Namcha Barwa in the east to Nanga Parbat on the west, about 1,500 miles, is divided into four sections by three meridional lines, (i) The Tista, (ii) The Kali and (iii) The Sutlej. The easternmost section, about 450 miles, is known as the Assam Himalayas, the next section of about 500 miles is the Nepal Himalayas, then a length of about 200 miles is the Kumaon Himalayas and the last about 350 miles form the Punjab Himalayas.

"Whilst in all the four parts the great range rises like a wall and the outer ranges tend to run parallel to it, no one portion of the Himālaya resembles another."

"In Nepāl we find numerous rivers cutting across the Great Himālaya range; in the Punjab between the Sutlej and the Indus we do not find one. In Népal the great peaks stand in clusters and rows; the great peak of the Punjab stands in solitude."

In considering the distribution of fishes along the south face of the Himalayas, there is one fact which appears most striking at the very outset, *i.e.*, the great variety of forms towards the east as compared with the case of the west. For instance, in the Brahmaputra and the Tista drainage systems all the genera of fishes enumerated above are found; while towards the west in the Gangetic drainage system we only find *Chaca*, *Amblyceps*, *Bagarius*, *Glyptothorax*, *Erethistes*, *Gagata*, *Nangra*, *Lepidocephalichthys*, *Nemachilus*, *Garra* and *Semiplotus*. Not one of these genera represents a highly specialised torrential form, and, with the exception of *Gagata*, *Nangra* and *Semiplotus*, all are widely distributed in the Oriental Region; the range of *Nemachilus*, *Garra* and *Glyptothorax* extends for a considerable distance towards the west. There is one genus of large Catfishes—*Sisor* Hamilton—which was recorded by Day from both the Indus and the Ganges systems; but it was found by Shaw and Shebbeare and Mukerji to occur also in the Tista river. In the Punjab Himalayas or the Indus drainage system *Chaca*, *Erethistes* and *Semiplotus* are absent. Unfortunately no systematic account of the Himalayan fishes has so far been published, and in the case of old records precise localities are not mentioned. In the case of *Semiplotus*, however, it may be noted that Day gave its distribution as "Assam, and Chittagong Hill ranges, as well as Burma", but recently

[1] Burrard, S. G. and Hayden, H. H.—*A Sketch of the Geography and Geology of the Himalaya Mountains and Tibet.* 2nd Edition, revised by Burrard, S. G. and Heron, (Delhi: 1933).

I[1] recorded *S. semiplotus* (McClelland) from the portion of the Nepal Himalayas drained by the Gandak. Though our present-day knowledge of the distribution of the Himalayan fishes is very imperfect, it is doubtful whether the special forms of the Assam Himalayas, such as *Balitora*, *Psilorhynchus*, *Parasilurus*, *Olyra*, *Pseudecheneis*, etc., will ever be found in the western Himalayas. These very genera or some other closely allied forms are found in Burma, Southern China, Siam, the Malay Peninsula and the Archipelago and Indo-China on the one hand and in the hills of Peninsular India on the other. It seems remarkable that the distribution of these eastern forms, instead of being continued along the Himalayas, is deflected from the limits of the Tista drainage towards the south. This most striking feature in the distribution of Indian fishes is explained later (*vide infra*, p. 255).

The records of distribution of the Himalayan fishes, as given above, support the hypothesis that I[2] have suggested elsewhere regarding the eastern origin of the freshwater fish fauna of India. The above series of genera represents various phases of migration of the fauna. For instance, in the case of such widely distributed genera as *Barbus*, *Labeo*, *Garra*, *Nemachilus*, *Lepidocephalichthys*, *Bagarius*, *Amblyceps*, etc., one has to imagine a large, deep river in low hills fed by small, broad, rocky tributaries. The wide distribution of these genera along the entire length of the Himalayan foot-hills shows further that such a river must have had a longitudinal course, like that of the Trans-Himalayan sections of the Brahmaputra and the Indus. It was, no doubt, during this type of drainage of the Himalayas that the large river fishes of India, such as *Catla* (represented in Siam and Indo-China by *Carpiocatla* Boulenger), *Cirrhina*, large-scaled Barbels, *Wallago* Bleeker, *Silonia* Swainson (replaced in Siam and Indo-China by *Pangasianodon* Chevey), *Pangasius pangasius* (Ham.), etc., could spread almost all over India. The presence in the Ganges, Brahmaputra and Indus of identical species of freshwater dolphins and turtles also shows the course and nature of this mighty river. Thus the distribution of the freshwater fish fauna of northern India lends a strong support to the existence of a river of the type of the Indobrahm, envisaged by Pascoe[3] and Pilgrim[4]. From the geological evidence it is concluded by these authors that such a river existed even in the Eocene period. Its lower course is evident from the distribution of the boulder conglomerates, but the position of its headwaters is a matter of mere conjecture. It is stated that the headwaters of the Indobrahm consisted of the Assam portion of the present-day Brahmaputra. Dr. C. S. Fox of the Geological Survey of India has pointed out to me in a note that this cannot be the case as

"A marine gulf in Burma and Upper Assam in Cretaceous times became an estuary in the Eocene and the mouth of a very important river in the Miocene. I do not see how

[1] Hora, S. L.—Notes on Fishes in the Indian Museum, XXIX. On a Collection of Fish from Nepal. *Rec. Ind. Mus.*, XXIX, pp. 45, 46 (1937).

[2] Hora, S. L.—Geographical Distribution of Indian Freshwater Fishes and its bearing on the probable land connections between India and the adjacent countries. *Curr. Sci.*, V, pp. 351-356 (1937).

[3] Pascoe, E. H.—Early History of the Indus, Brahmaputra and Ganges. *Quart. Journ. Geol. Soc.*, LXXV, p. 136 (1919).

[4] Pilgrim, G. E.—Suggestions Concerning the History of the Drainage of Northern India. *Journ. As. Soc. Bengal* (N. S.), XV, p. 81 (1919).

the debouchure of a river into a delta can become the source of a river that is to go to sea all the way round the Himalayan foothills to the Indus."

In the same note he stated that

"It is probable that as the old geosyncline of the Himalayan belt was folded up into a mountain chain a depression was established parallel to it to the south. In the swampy country the rivers from the rising hills discharged, and their silt was spread out laterally into great alluvial fans. It is these Siwalik deposits of freshwater fluviatile deposition that have been joined up lengthways, along the axis of the depression, and thus have supplied material for the belief in a Siwalik river."

This view is, however, disputed by Wadia[1] who has drawn attention to the remarkable homogeneity and uniformity of the Siwalik deposits all along this strike, from Assam to the Punjab. This strike continuity is inconsistent with the fan theory of deposition at the mouths of isolated transverse streams and is best explained by deposition in a continuous longitudinal basin of a wide east-west flowing river.

Without going into the geological merits of the case, it seems clear that the distribution of freshwater fishes, as indicated above, postulates the existence of a mighty river of the nature of the Indobrahm.[2] This river at an early stage of its existence certainly did not have its headwaters in the Assam portion of the present-day Brahmaputra, but it must have crossed the broad isthmus that joined India with the main Asiatic continent and had its headwaters further east. The distribution of the large freshwater river fishes of the Oriental Region (*vide supra*, p. 254) can only be explained on this assumption. Even the occurrence of precisely the same river fishes, especially of the giant forms as *Catla catla* (Ham.), *Labeo rohita* (Ham.), *Cirrhina mrigala* (Ham.), *Wallago attu* (Bloch), *Pangasias pangasias* (Ham.), *Silonia silondia* (Ham.), and others in Burma, Assam, Bengal, the United Provinces, the Central Provinces, Orissa and the Punjab postulates the existence of a large, longitudinal river and its subsequent divisions into several independent watersheds. As the Himalayas rose to a great height in the region of this isthmus (mostly the western part of the Assam Himalayas and eastern part of the Nepal Himalayas) all the evidence concerning the north-eastward extension of the Indobrahm seems to have been obliterated. The uplift movement was probably most active in this region as we find practically all the highest peaks of the Himalayas clustered round this area. This differential movement, which probably occurred late in the Miocene period, must have obliterated all traces of the eastward extension of the Indobrahm and also acted as a barrier between the eastern and the western Himalayan fishes. The new stocks of specialised hill-stream fishes from the east, not finding means to cross this barrier, were deflected towards south-west along the Satpura Trend which probably at this period stretched across India as a pronounced

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[1] Wadia, D. N.—The Tertiary Geosyncline of North-West Punjab and the History of Quaternary Earth-movements and Drainage of the Gangetic Trough. *Q. J. Geol. Min. Met. Soc. India*, IV, pp. 69-96 (1932).

[2] Evidence of the existence of the Indobrahm is also furnished by "the tendency of the tributaries of the supposed Indobrahm to flow in a direction opposite to that of the modern trunk river. If but one feeder has been observed to take a course contrary to that of the main stream, it might have been attributed to some local accident of topography, but when all the principal affluents of a long section of the river do so, it is indicated that the Indobrahm flowed from east to west, when the tributaries were developed, and that its direction of flow has been reversed." (Burrard, Hayden and Heron, *op. cit.*, p. 349.)

range from Gujarat to the Assam Himalayas. From Gujarat the hill-stream fauna migrated towards the south along the Western Ghats and spread to the hills of the Peninsula in the extreme south. It may here be noted that the Indobrahm fauna of moderate, deep currents does not extend to the south below the Kistna river, while the torrential fauna of the Eastern Himalayas is represented in the hills of the extreme south of the Peninsula by forms such as *Silurus* Linn., *Bhavania* Hora, *Parapsilorhynchus* Hora, *Thynnichthys* Bleeker, etc.; it is not found in Ceylon, for the island had by then become separated from the mainland. Further, it has no representative in Africa, because the main land bridge between Peninsular India and Africa had already disappeared during the Eocene period, though a mass of land in the region of the Gulf of Oman probably existed till Pliocene or possibly even Pleistocene times.[1] This course of events, in my opinion, explains the anomalous distribution of the various hill-stream fishes of India, and suggests a reason for the closer similarity of the South Indian fish fauna with that of the Malay Peninsula and the Archipelago.

To the west of this supposed barrier in the Eastern Himalayas the hill-stream fauna is composed of ordinary rapid water fishes; most of the genera are more or less uniformly distributed all along the range. In the Nepal Himalayas, however, the eastern element, *Semiplotus*, *Chaca* and *Erethistes*, is more pronounced. The last two genera extend up the Ganges system and are absent from the Punjab Himalayas. The Punjab Himalayas, being furthest from the source of distribution, has the least number of hill-stream forms in its fauna. It may, therefore, be presumed that at the end of the Kumaon Himalayas or somewhere in that region there is probably another barrier, which isolated the fauna of the Punjab at a fairly early age. This conclusion is justified by the detailed studies recently carried out by Mukerji[2] and Hora[3] on the specific position of some of the Himalayan fishes. The isolation of the Punjab Himalayan forms may have resulted through the differential earth-movements which elevated the Potwar basin into a plateau and led to further dismemberment of the Indobrahm into the Indus and the Ganges systems of the present-day drainage of the Himalayas. In any case, this barrier must have been formed at a later date and is not contemporaneous with the Eastern Himalayan barrier. This presumption is based on the fact that after the formation of the Eastern Himalayan barrier there was for some time no river of the nature of the Ganges flowing into the Bay of Bengal to divide the Peninsula from the Extra-Peninsula: such a river, if it had existed, would in itself have acted as a barrier and have inhibited the dispersal of Himalayan fishes to the hills of the Peninsula. It is thus seen that the Indobrahm must have continued to flow towards the Arabian Sea even after the severence of its

[1] Wiseman, J. D. H. and Sewell, R. B. S.—The floor of the Arabian Sea. *Geol. Mag.*, LXXIV, pp. 219-230 (1937).

[2] Mukerji, D. D.—Report on Burmese Fishes collected by Lt.-Col. R. W. Burton from the tributary streams of the Mali Hka river of the Myitkyina District (Upper Burma). *Journ. Bombay Nat. Hist. Soc.*, XXXVII, pp. 49-59 (1934).

[3] Hora, S. L.—On a further Collection of Fish from the Naga Hills. *Rec. Ind. Mus.*, XXXVIII, pp. 320-324 (1936).

connection with the Far East; its dismemberment seems to have occurred in several stages. After the formation of the Eastern Himalayan barrier its headwaters may have been in the Nepal Himalayas. A later upheaval probably divided it into a westerly flowing Indus and an easterly flowing Ganges. The formation of this drainage pattern has a counterpart on the northern face of the Himalayas also, namely, the reversal of the direction of flow of the Tsangpo towards the east and the westerly flowing Indus.

From the distribution of the fish fauna along the southern face of the Himalayas it is thus possible to recognise three well marked divisions—the Eastern Section up to and including the drainage basin of the Tista river, the Middle Section up to the Sutlej river and then the Western Section comprising the entire drainage basin of the Indus. The precise boundaries of these sections can only be demarcated when our knowledge of the various Himalayan species and their races becomes more exact. It may be indicated that the Jumna river was a tributary of the Sutlej not very long ago, though it now joins the Ganges. The oscillation of the Jumna makes it still more difficult to define the various sections without a proper survey of the fish fauna of the Himalayas.

Himalayan Fishes and their Bearing on the Evolution of the Present-day Drainage System of the Himalayas.

With the exception of *Oreinus* and *Nemachilus*, none of the genera enumerated above are found on the northern face of the Himalayas, the fish fauna of which comprises the Schizothoracinae, *Glyptosternum* McClelland and *Nemachilus*. In another place I[1] have shown that the Nemachili of the northern and the southern faces of the Himalayas are very distinct from each other and that *Glyptosternum* is very different from the other Glyptosternoid fishes found in Siam, S. China, Burma and the Eastern Himalayas. *Oreinus* is a mountain form of *Schizothorax* Heckel and is only found along the slopes of the Central Asiatic plateau, but not on the tableland. In fact, it may definitely be stated that there is no similarity between the fish faunas of the northern and the southern faces of the Himalayas. To account for this I have suggested that the two faunas were probably evolved from the same stock at different geological ages and owing to the barrier provided by the rising Himalayas had little chance to intermingle. The deep gorges and rapids in the course of certain Himalayan rivers with trans-Himalayan courses still isolate the two fish faunas from each other.

With regard to the evolution of the present-day Himalayan drainage pattern two alternative theories have been advanced.

> "One of the theories postulates that at an early age the Himalaya had ordinary consequent drainage, the rivers flowing north and south from the crest. This simple drainage pattern is considered to have been modified to its present form by some of the south-flowing rivers cutting back through the range and capturing rivers on the Tibetan side. The much greater precipitation on the south side of the range and the much steeper fall and therefore greater erosive power are put forward as possible reasons for the unusual behaviour of the south-flowing rivers. The alternative theory postulates that the Arun and similar rivers always had their present courses which, when they were inaugurated, were the easiest routes down an irregular surface sloping towards the

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[1] Hora, S. L.—Comparison of the Fish-Fauna of the northern and the southern faces of the great Himalayán range. *Rec. Ind. Mus.*, XXXIX, pp. 241-250 (1937).

Gangetic plain. Subsequently the Himalayan range is considered to have risen up across the rivers, but so slowly that by vigorous erosion they were able to keep open their original channels."[1]

The distinctness of the northern and the southern fish faunas of the Himalayas definitely favours the former view. If the rise of the Himalayas had been so slow as to enable the rivers to keep open their channels by vigorous erosion there should have been little or no difference in the fish faunas of the cis- and trans-Himalayan portions of such rivers as the Brahmaputra, the Arun, the Sutlej, the Indus, etc. On the other hand, there is every reason to believe that the rise of the Himalayas was in sharp orogenic movements so that the fishes of the southern face of the range were unable to adapt themselves to very turbulent waters and have, even to this day, remained confined to low valleys and are rarely found above an elevation of four to five thousand feet. In this connection it may also be remembered that the so-called Indian monsoon conditions—south-west for four months and north-east for three or four months—had begun before the Himalayas started to rise, as in the late Cretaceous period open seas of great extent existed to the south of India and some land had been formed to the north. The rise of the Himalayas had a great influence on the distribution of rainfall, for most of the moisture is now precipitated on its southern face; and there is practically no rainfall on the northern face of the Himalayas. Consequently, the rivers along the southern face are very turbulent while those on the northern face are placid, broad-valleyed and deep. Very different sets of ecological conditions were thus produced on the northern and southern faces of the Himalayas and these became accentuated as the mountains rose higher and higher.

When the south-flowing rivers, through erosion captured the rivers on the Tibetan side it was natural that some of the fishes on the Tibetan side should have been washed down on the southern side, but they had to pass through such precipitous channels before reaching congenial conditions that with the exception of one genus of the Schizothoracinae—*Oreinus*, a specialised member of the subfamily fully adapted for life in rapid, mountain streams—no other member of the Central Asiatic fauna has been able to colonise the southern slopes of the Himalayas.

The migration of torrential fishes along the southern face of the Himalayas and from the Eastern Himalayas to the hills of the Peninsula shows that the process of river-capture was a fairly common phenomenon in this territory and also in the region of the contiguous hill-ranges to the east. The distribution of specialised hill-stream fishes strongly suggests that in south-eastern Asia, as a rule, the rivers on the west beheaded the rivers on the east[2] and thus effected the transference of the fish fauna from the east to the west.

SUMMARY.

The physical and biological factors that govern the life of a torrential fauna are examined and it is indicated that the distribution of highly

[1] Wager, L. R.—The Arun River Drainage Pattern and the rise of the Himalayas. *Geog. Journ.*, LXXXIX, pp. 239-250 (1937).

[2] Gregory, J. W.—The Evolution of the River System of South-Eastern Asia. *Scottish Geog. Mag.*, XLI, pp. 129-141 (1925).

specialised hill-stream fishes cannot be effected by the ordinary methods of dispersal; it has to be explained in terms of longitudinal valleys, river-captures and tilting of mountain blocks.

The distribution of the fish-genera along the southern face of the Himalayas is discussed in terms of the ecological associations of the different types, and it is indicated that at a very early period of the rise of the Himalayas a mighty longitudinal river must have existed along its base. This river probably corresponded with the 'Indobrahm' of Pascoe and Pilgrim, but the distribution of fishes shows that it must have extended towards the Far East. From the distribution of various fishes the probable phases of dismemberment of this river are indicated, and it is explained how the Himalayas became divided hydrographically into three main divisions—the Brahmaputra, the Ganges and the Indus drainage systems.

The almost total dissimilarity between the northern and the southern Himalayan fishes is indicated, and it is concluded therefrom that the present-day drainage pattern of the Himalayas cannot have resulted from an antecedent drainage, according to which the Himalayan range is considered to have risen up across the rivers which kept their original channels open by vigorous erosion, but is the result of consequent drainage, of which the southern rivers captured the rivers of the north secondarily.

Geographical Distribution of Indian Freshwater Fishes and Its Bearing on the Probable Land Connections between India and the Adjacent Countries.*

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THE relationships and the geographical distribution of the freshwater fishes of India were discussed by two of the leading ichthyologists, Day[3,4]† and Günther[7], of the last century. The former advocated Malayan affinities for the Indian fauna, while the latter, though admitting the migration of several Oriental freshwater fishes to Africa, laid special stress on the African affinities of this fauna. Beyond some casual references[1,2] very little work has since been done on this aspect of the Indian freshwater fishes, and in view of the advances that have been made in our knowledge of the paleogeography and systematics of fishes it seems opportune to review the whole subject in the light of recently discovered facts.

A freshwater fish lives entirely in freshwater, both in the young and adult stages, and never descends to the sea. The above definition excludes all anadromous fishes which are essentially marine but ascend freshwaters for breeding and the catadromous fishes which are essentially freshwater forms but descend into the sea for similar purposes. As the freshwater fishes are generally restricted to the water courses in which they live, they form a very important group for the elucidation of the paleohydrographical relationships of adjacent lands. Watersheds in the case of these fishes form effective barriers so long as their positions remain unchanged; the process of river-capture, however, may facilitate their migration in one direction but not in the other. There is an unfortunate impression, mainly among geologists, that in the case of fishes dispersal may be effected through the agency of birds, chiefly aquatic species, which may carry the eggs attached to their feet from one watershed to another. Those, who have paid particular attention to this matter, however, are definitely of the opinion that such a mode of dispersal of freshwater fishes is normally highly improbable, even though there may be records of such fortuitous dispersal in practically all groups of animals including freshwater fishes.

In connection with my work on the Siluroid fishes of India for a revised edition of "Fishes" in the *Fauna of British India* series, I have been greatly struck by the close similarity of the Indian forms to those found towards the east in Indo-China, Siam, and the Malay Archipelago. As a result of a detailed study of the genera and species inhabiting these regions I am definitely of the opinion that the freshwater fish fauna of India in the main originated in South-eastern Asia, most probably in Indo-China, and spread westwards by successive waves of migration to India and later to Africa while the two masses of land were connected with each other. Gregory's researches[5,6] on the evolution of the mountain and river systems of South-eastern Asia have shown that in this region there were extensive river captures—the rivers on the west beheading the rivers on the east; these changes made possible the migrations of aquatic animals from the east to the west but not in the reverse direction. Gregory's researches have further shown that all the rivers of Eastern Tibet drained into the Gulf of Siam or the South China Sea before the present river systems became established, and this bears out Pelseneer's view.[12,13] The freshwater fauna of Eastern Asia at least may have originated along the coasts of Indo-China, when the ocean water in this area was greatly diluted by the drainage into it of several river systems.

Professor Gregory's views about the capture of the eastern rivers by the western rivers are, however, not accepted by all geologists, for there is a general belief that the Brahmaputra and the Irrawaddy-Salween systems were separated in the Pre-Eocene period by the Tethys Sea and in the Post-Eocene days by the newly upheaved Himalayas, the Patkoi Range and the Arakan Yomas. According to these views there could not

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† Numerals refer to the corresponding numbers in the list of references at the end of the article.

any migration of freshwater faunas by a system of river-captures, except perhaps during the transition periods, between the Indo-Chinese rivers and the Indian rivers. Further there is no geological evidence for the Indian rivers having originated in Burma. Some of the peculiarities in the distribution of Indian freshwater fishes may be explained on the supposed existence of the Siwalik or the Indo-Brahm River,[11,14,18] but a considerable mass of evidence bearing on the close relationship and distribution of the fishes of South-eastern Asia demands for its explanation a hypothesis similar to that worked out by Gregory. This mass of evidence is so striking and convincing that it may be worth-while for the geologists to re-examine their data regarding the Cretaceous-Tertiary land connections between India and the Far East.

Mori[10] has recently stressed the Oriental affinities of the fish-fauna of the Upper Yangtse-Kiang which comprises an abundance of the Siluroidea, the Homalopteridæ, the Ophicephalidæ and a large number of Indian genera of the Cyprinidæ. These results fully support Gregory's work according to which the Upper Yangtse-Kiang at first drained into the Red River but later turned northeastwards across Central China to the East China Sea. Only such a course of events could account for the presence of Oriental genera in the Upper Yangtse-Kiang and the Palæarctic genera in its middle and lower portions. According to Mori's researches the Nan Shan Mountain Range divides China into the northern Palæarctic subregion and the southern Oriental subregion.

As a comprehensive example of the east to west migration of the aquatic fauna, one may consider the evolution and distribution of the family Schilbeidæ* which is represented both in the Oriental and the Ethiopian regions by a number of genera. Of the 19 or 20 genera of the family that can be recognised at the present day there is not one that is common to the two regions. If it be conceded that the ancestors of the Schilbeidæ were devoid of barbels and teeth in the jaws, it naturally follows that the African genera, usually with eight barbels and a well-developed dentition, represent a fairly specialised and more highly evolved branch of the family; African genera such as *Ansorgia* Boulenger, with only one pair of mandibular barbels, and *Siluranodon* Bleeker, with no teeth in the jaws, are retrogressive forms as compared with the primitive genera found in the Far East. I believe that *Pangasianodon* Chevey, represents the least specialised form of the family; this genus is found in Indo-China and is characterised by the possession of two minute maxillary barbels, a large air-bladder and no teeth. *Silonia* Swainson, of the Indian waters, also possesses two minute barbels, but owing to its highly predaceous habits, it has developed large caniniform teeth both in the jaws and on the palate. Due to the reduction of its body cavity by the greater development of the caudal region and the lateral compression of the body the air-bladder is greatly reduced. In Peninsular India some less specialised, *Silonia*-like fishes became further modified and developed two additional mandibular barbels; they possess caniniform teeth and a long anal fin but the air-bladder is not so greatly reduced as in *Silonia*. For this new type I have proposed the name *Silonopangasius*.† So far as can be judged at present this line of specialisation only extended as far as the extreme west of Peninsular India.

Pangasianodon-like ancestors also gave rise to forms like *Helicophagus* Bleeker and *Pangasius* Cuvier and Valenciennes; the latter is found from Indo-China to India, while the former, in which the dentition is only partially developed, is found only in the Far East and is absent from Burma and India. Though there are several species of *Pangasius* in Indo-China, Siam and the Malay Archipelago, in Indian waters it is represented by a single, very highly specialised form. Here again the specialisation in form occurs as one proceeds from the east to the west.

In Siam and the Malay Archipelago *Helicophagus* gave rise to the genus *Laides* Jordan (= *Lais*, 6 barbels); possibly *Laides* evolved into *Pseudeutropius* Bleeker (8 barbels) in the Malay Archipelago; the latter genus is also found in India. Certain members of *Pangasius*, probably more specialised as regards dentition, gave rise in Siam to *Platytropius*,* a new genus wi[th] extensive patches of vomero-palatine teet[h]

* For a detailed treatment of the classification, distribution, ecology and evolution of the Schilbeidæ reference may be made to my paper, shortly to be published in the *Records of the Indian Museum*.

† Genotype: *Ageneiosus childreni* Sykes, 1841.

* Genotype: *Pseudeutropius siamensis* Sauvage, 1883.

and with a flattened head and air-bladder, and in India to *Proeutropiichthys*,† a new genus for species of *Pseudeutropius* with four patches of teeth on the palate. In the Indian waters *Pseudeutropius* gave rise to *Ailia* Gray and *Proeutropiichthys* to *Eutropiichthys* Bleeker; the latter genus is also know from Siam. Probably *Platytropius* gave rise to *Clupisoma* Swainson of the Indian Waters. From the primitive stock that gave rise to *Proeutropiichthys*, probably developed all the Schilbeid genera of Africa, at a stage when the mandibular barbels were considerably behind the tip of the lower jaw and were not situated in a straight line. So far no intermediate forms have been discovered between the Indian *Pseudeutropius* (*sensu lato*) and the African *Eutropius*. As the difference in the two forms consists mainly in the position of the mandibular barbels, no palæontological records will ever be able to bridge the gulf between the Indian and the African Schilbeidæ. There is, however, little doubt about the close genetic affinities of the Indian and the African genera of the Schilbeidæ.

According to Regan[16] "The distinctness of the African and the Indian Schilbeidæ makes it probable that this family was established in both regions in pre-tertiary times." The probable history of the dispersal of the Schilbeidæ as understood by me makes it clear that this family must have extended its range to Africa before the two continents became disconnected, probably during or after the Eocene.

The facts detailed above concerning the geographical distribution of the Schilbeidæ are opposed to the theory of permanence of oceans and continents, as they can only be explained by the existence of connected water courses, through either river-captures, commingling or otherwise, over a land connection between India and Africa. Whether this connection was in the form of a "land-bridge" between the two continents, or the two land-masses were merely juxtaposed at some remote period and later drifted apart, it is very difficult to decide. It seems clear, however, that even during the Eocene South India and Africa had land-connections which permitted a dispersal of freshwater fishes from the former the latter country. The abrupt in the African and the Indian Schilbeidæ is certainly the result of some form of isolation since a fairly remote period, and before this occurred presumably the Indian forms were of the same type as those now found in Africa. The higher specialisation of the Indian genera can be accounted for by the fact that India was a centre of great disturbance during the Tertiary period owing to the earth-movements that gave rise to the Himalayas, whereas Tropical Africa with its large lakes provided a stable environment for its fauna and the specialisations of the Schilbeidæ of this region can definitely be correlated with life in comparatively calm and clear waters.

There is also a belief that the Ostariophysi, the class to which Catfishes and Carps belong, originated in the north and spread southward to different continents. This hypothesis would explain the occurrence of allied genera both in India and Africa without the aid of a land connection between the two countries. Regan[16] has already pointed out that this view "involves so many improbabilities as to be almost unbelievable." The mode of dispersal of the Schilbeidæ as detailed above is strongly opposed to the northern origin of the Ostariophysi and appears to be entirely in accord with the recent geological work on the river and mountain systems of South-eastern Asia.

While discussing the African element in the freshwater fauna of India Annandale[2] remarked: "Doubtless the three territories (*i.e.*, Africa, S. America and India) had then a very similar freshwater fauna, but there is some evidence that Africa was its centre of distribution." Unfortunately he made no reference to this evidence, and in view of what is stated above it seems almost impossible to believe that the freshwater fauna of India was at any stage, at least during the Tertiaries, invaded by that of Africa.

Prashad[15] from his study of the recent and fossil Viviparidæ (Mollusca: Gastropoda) came to the conclusion that "Peninsular India forms the central zone whence the Viviparids of Asia and Africa are derived." At the present day, so far as freshwater fishes are concerned, Peninsular India contains many primitive forms, and thus superficially it may appear to be a centre of origin of the common Indo-African fauna, but the taxonomic and paleogeographical evidences adduced above show that the fresh-

† Genotype: *Eutropius macrophthalmus* Blyth, 1860.

water fish-fauna of Peninsular India was itself derived from that of South-eastern Asia.

The close relationship between certain highly peculiar genera of Indo-China and India, such as *Carpiocatla* Boulenger, and *Catla* Cuvier and Valenciennes; *Parapseudecheneis* Hora and *Pseudecheneis* Blyth, *Gyrinocheilus* Vaillant and *Psilorhynchus* McClelland; etc., etc., and the distribution of *Silurus* Linnæus and the Homalopteridæ also prove conclusively that there has been an east to west migration of the freshwater fauna in South-eastern Asia. The older genera, such as *Mastacembelus* Cuvier and Valenciennes, *Notopterus* Lacépède, *Labeo* Cuvier, *Barbus* Cuvier and Valenciennes, *Barilius* Hamilton, *Heterobranchus* Geoffery, *Clarias* Gronovius, etc., which are common to Africa and the Oriental region, probably spread from India to Africa at the time of the Cretaceous buckling which, according to Gregory[6] (p. 134), "produced a series of continental valleys trending east and west fragments of which still survive in Africa in the basins of the Zambezi, the middle Congo, and the northern section of the Niger." The physiography of India, however, underwent considerable changes during the Tertiary period.

In elucidating the geographical distribution of animals, great significance is generally attached to the occurrence of the same genus or species on two distinct land masses. According to the more or less accepted views on evolution a species or a genus can exist unchanged through millions of years only if there had been no change in its *milieu* throughout this period. Even gradual changes in the environment of an animal induce fine adjustments on the part of the organism.[8] Any small changes of organisation are utilised by taxonomists in their system of classification. As the science of taxonomy progresses, animal structure is bound to receive closer and closer scrutiny, with the result that a genus occurring over a wide area will be found to consist of several well-defined groups. Isolation and segregation are two very important factors in the production of new forms,[17] and it seems highly desirable, therefore, to pay more attention to the interrelationship of the seemingly divergent genera of different landmasses rather than to look for precisely identical animals in their fauna. The converse is also true. In the case of similar forms occurring in two widely separated places convergent evolution should not be invoked unless no other explanation seems possible. In the two sets of genera mentioned above the truth of these remarks is clearly brought out.

So far I have referred only to the Far Eastern genera that are found in the Indian waters. There is, however, one genus *Etroplus* Cuvier and Valenciennes of Peninsular India and Ceylon which has its close allies only in Madagascar. Günther[7] accounted for its occurrence in India as follows: "*Etroplus* inhabits Southern and Western India and Ceylon, and has its nearest ally in a Madagasse Freshwater fish, *Pareutroplus*. Considering that other African Chromides [Cichlidæ] have acclimatised themselves at the present day in saline water, we think it more probable that *Etroplus* should have found its way to India through the ocean than over the connecting land area; where, besides, it does not occur." I am in agreement with Günther's supposition and believe that *Etroplus* came to India *via* the sea and, after becoming a freshwater form, probably along the Malabar Coast, it remained confined only to the south-western part of the Peninsula, as the rivers of this area probably never became connected with the Indus and the Ganges systems. Further, it seems probable that *Pareutroplus* Bleeker and *Eutroplus* are derived from a common Cichlid ancestoral form that wandered across from the east coast of Africa to Madagascar and South India where they became acclimatised to freshwater conditions independently.

It is generally believed that the land connection between India and Africa disappeared somewhere about the transition period between the Cretaceous and the Tertiary. It is during the obscure interval between the Cretaceous and the Tertiary that nearly all the modern types of bony fishes originated. Regarding the freshwater Catfishes (Siluroidea), to which the Schilbeidæ belong, there is no evidence that they are of any great antiquity; their first known appearance is indicated by some fossils in the Tertiary deposits of the Siwalik and the highlands of Pedang in Sumatra, where remains of some of the living genera have been found. I have referred above to the continuity of distribution of Schilbeidæ from Indo-China to Africa, the same is true of the Catfishes of the families Clariidæ and Bagridæ. The

lariidæ live in mud in marshy areas of both countries and have thus retained their primitive habits. On account of this we find that *Heterobranchus* and *Clarias*, the two oldest members of the family, are common to the two continents. Tropical Africa with its vast stretches of ancient lakes provided a more suitable *milieu* for these fishes, some of which took to a burrowing mode of life. Consequently they became eel-shaped and their accessory respiratory organs and the associated skeletal elements became degenerate. In India, on the other hand, the conditions were very unstable during the Tertiary period, with the result that the primitive genus *Heterobranchus*, of which fossil remains have been found in the Siwalik formations of the Lower Pliocene, disappeared altogether and only one highly specialised species of *Clarias*,[9] *C. batrachus* Linn., is now found throughout India, while two other less specialised forms, *C. brachysoma* Günther and *C. dayi* Hora, are confined to Ceylon and the Wynaad Hills respectively.

The Bagridæ, like the Schilbeidæ, became established on both the continents at an early date and after the severance of the connection between the two lands evolved independently so that at the present day there is no genus common to the two regions. However, a close parallelism exists between the forms inhabiting similar situations on the two continents. *En passant* it may also be remarked that most of the other Siluroid families of India and Africa are evolved from the Bagridæ.

A remarkable feature of the Schilbeidæ is that no member of the family is found in Ceylon, which may be due to the fact that Ceylon became separated from India at a stage earlier than the disappearance of the land connection between India and Africa. The absence of the Schilbeidæ from Ceylon may also be explained on the assumption that at some period the water courses changed in such a way that in spite of the land connection between India and Ceylon no migration from the north to the south could take place. It is thus seen that unlike the distribution of the land animals, where probably the climatic considerations are of greatest importance, the aquatic animals are bound within their watersheds and in spite of land connections and favourable climatic conditions between two adjacent lands may not spread from one to the other if their water courses had no chance to become continuous at some period or another. The distribution of fishes, therefore, though extremely important in zoogeographical studies, has thus only a limited value in elucidating the extent of the former land and sea connections.

In this east to west migration of the fauna I have assumed throughout that India was connected with the Far East, at least from the late Cretaceous onwards. This connection was of a very different nature from what it is to-day, for in the early Tertiaries a considerable part of Northern India was under the sea. The Bay of Bengal is considered to be an ancient feature of the physiography of India, so that the old connection between India and the Far East probably stretched over the Peninsula through the coal-field areas of Bengal to the Assam Hills, North Burma and beyond. At certain periods the direct land connection between Assam and Burma was cut off by an arm of the sea, but still Assam remained connected with the Far East through Tibet and Southern China. The distribution of the Indian freshwater fishes affords ample evidence in support of these routes of migration.

I may also refer here to the remarkable similarities between the faunas of the Malay Archipelago, Malabar Zone of South India and Tropical Africa. To account for these anomalies of distribution several workers have been led to establish a southern continent including South America, but of which Madagascar did not form a part. In my opinion when the primitive forms were spreading from Indo-China to Africa they sent branches to the south in all areas over which they passed, and as these southern extremities were away from the main centre of disturbance (the Himalayas) and also somewhat out of the way of the succeeding waves of migration they continued to harbour primitive animals in, what one may say, these corner seats. The islands of the Malay Archipelago, such as Java, Sumatra, Borneo, etc., the Malabar Zone of India and West and South Africa to-day form the limits of the ancient waves of migration and consequently contain many primitive forms, which, owing to the severance of land connections, could not spread any further. Of the genera I have referred to above, *Heterobranchus* of the Clariidæ shows a discontinuous distribution as it is

found in Africa on the one hand and in Banka and Borneo on the other. There is no doubt that even in the Lower Pliocene period its range of distribution must have been more or less continuous, as fossils are known from the Siwalik formations of that period.

It seems highly probable that the southward migration of the Indo-Chinese fauna in the region of the Malay Archipelago must have followed the course of the Indo-Malayan Mountains and of the Malay Arc[5] by a series of river-captures. The strong similarity between the fauna of South India and that of the Malay Archipelago[5] is probably not due to the migrations of the forms *inter se* but to their common origin from an east to west migrating, primitive stock.

In the above discussion I have not taken into consideration the route of migration that now exists between North-western India, through Baluchistan, Persia, Mesopotamia, Palestine, etc., to Africa. This route is known as Jocobi's Arabian region of dispersal and does not seem to have played any important part in the interchange of the freshwater faunas from Africa to India. Some of the Indian forms, however, such as *Glyptothorax* Blyth, *Garra* Hamilton, etc., have undoubtedly spread westwards along this route. *Scaphiodon* Heckel appears to be the only form that may have spread from Persia, Baluchistan and Sind to the Western Ghats.

To sum up it may be stated that the evidence provided by the distribution of the freshwater fishes of India indicates an eastern origin of the fauna and its subsequent dispersal to the west. The close relationship between the Indian and the African freshwater fishes can only be explained on the assumption of a land connection between the two countries. The absence of the Schilbeidæ from Ceylon and their presence in Africa suggests that Ceylon may have become separated from India at a stage earlier than the severance of the land connection between Africa and India. The distribution of freshwater fishes shows that Peninsular India had a land connection with the Far East, at least from late Cretaceous onwards, and probably at no time during this interval it became an island. The similarity in the faunas of South and West Africa, South India and the Malay Archipelago are probably due to the fact that they received branches of the primitive stock when it was migrating from the east to the west along a northern and a considerably more disturbed part of the Oriental region. The above review of the subject clearly shows that there is no African element in the freshwater fish-fauna of India. The existing connection of Africa with North-western India is comparatively of a much more recent date and does not seem to have played any important part in the dispersal of the freshwater faunas.

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ON THE AGE OF THE DECCAN TRAP AS EVIDENCED BY FOSSIL FISH-REMAINS.

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On the Age of the Deccan Trap as Evidenced by Fossil Fish-Remains.*

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AT the discussion on the age of the Deccan Trap, held at the Hyderabad (Deccan) meeting of the Indian Science Congress, several speakers referred to the great stratigrahpical value of the Inter-trappean fossils, and casual references were made by Crookshank, Sahni and the writer to the fossil fish-remains discovered from the inter-trappean beds. Since then the extensive material collected by Mr. H. Crookshank from the inter-trappeans of Deothan and Kheri has been worked out, though the results[2] have not yet been published. A few fossil scales from the inter-trappeans (Lameta ?) at Dongargaon,[3] Takli and Paharsingha, collected by Rev. Hislop and now preserved in the collection of the Geological Survey of India, have also been examined; these very fragmentary remains had not hitherto been studied by any specialist. Some fossil scales from the infra-trappean bed at Dhamni, east of Warora, collected by Mr. F. Fedden have also been examined. The present investigation, when combined with that of A. S. Woodward's (1908) on the fossil fish-remains from the Lameta beds at Dongargaon, throws considerable light on the probable age of these beds.

From a stratigraphical point of view the results obtained so far may be tabulated as follows :—

Name of bed	*Type of fish*	*Geological Horizon*
Lameta, Dongargaon	*Lepidosteus indicus* A. S. Woodw.	Typically tertiary; Lower Eocene to present day in America.
,, ,,	*Pycnodus lametæ* A. S. Woodw.	Not later than close of Eocene.
,, ,,	*Eoserranus hislopi* A. S. Woodw.	Tertiary.
(?) Inter-trappean (possibly Lameta), Dongargaon.	*Clupea* sp.; scale.	" Not known from below the Upper Eocene " (Zittel).
Infra-trappean, Dhamni.	*Clupea* sp.; scales.	Do.
Inter-trappean, Paharsingha.	*Lepidosteus* spp.; scales.	Tertiary.
Inter-trappean, Takli.	*Nandid* scale.	Fossils of the family not known.
Inter-trappean, Deothan and Kheri.	*Clupea* spp.; scales.	As known at present from Upper Eocene to recent.
Do.	*Musperia* sp.: scales.	Old Tertiary.
Do.	Cyprinid scale.	Lower Eocene to recent.
Do.	Polyacanthid scale.	Fossils of the family not known.
Do.	*Serranus* sp.	Tertiary to recent.
Do.	*Nandus* sp.	Fossils of the family not known.
Do.	*Pristolepis* sp.	Do.

In all 10 principal types of fish have been discovered so far from the trappean beds. Of these, *Lepidosteus* and *Pycnodus* are Ganoid fishes which " exhibit their greatest development in Palæozoic, Triassic and Jurassic formations; and from the base of the Cretaceous system upwards they become more and more replaced by the bony fishes. The few still existing Ganoids live either exclusively, or at least partly, in fresh-water, while the large majority of the fossil forms occur in purely marine deposits. As a rule, only the Devonian and Tertiary Ganoids occur in fresh-water formations." From India, however, the remains of fresh-water Ganoids are known from the Kota Maleri beds of the Mesozoic period, from the Lameta beds at Dongargaon and from the Inter-trappeans[4] at Paharsingha. About

* Read in the Geology Section at the Jubilee Session of the Indian Science Congress held at Calcutta, and published with permission of the Director, Zoological Survey of India.

[2] The detailed results of these investigations will be published in the *Records of the Geological Survey of India.*

[3] A scale of *Clupea* sp. in the collection of the Geological Survey of India is registered as having been obtained by Rev. Hislop from the inter-trappean bed at Dongargaon. Mr. H. Crookshank, however, informs me that, as far as known, there are no inter-trappean beds at Dongargaon [illegible] Lameta beds.

[4] Since the above was written, Mr. S. R. Narayan Rao has discovered the remains of *Lepidosteus* scales in the inter-trappean bed at Kateru near Rajahmundry. Through the kindness of Prof. B. Sahni, I was given an opportunity to examine the Kateru specimen.

Lepidosteus Woodward (1908) observed that it is "typically Tertiary, differing essentially from the numerous secondary Ganoids to which it is related, by its highly specialised vertebræ. It ranges from the Lower Eocene to the Lower Miocene in Europe, and from Eocene to the present day in North America." With regard to *Pycnodus*, he stated that "according to European standard, cannot be later than the close of the Eocene." *Eoserranus* is a Percoid fish of a very primitive type, as its scales have not assumed the typical features of the modern Acanthopterygian fishes. Woodward says that "No true Percoid has hitherto been recognised in a typically Cretaceous formation in any part of the world." Accordingly, he fixed the age of the Lameta fish-fauna of Dongargaon to be between the Danian Cretaceous and the Upper Eocene.

From the inter-trappean (Lameta ?) bed at Dongargaon, Hislop collected a nicely preserved scale of *Clupea* Linn. in which the transverse radii are complete and well marked. According to Zittel, *Clupea* is "not certainly known below the Upper Eocene of Monte Bolca, near Verona." This record would seem to fix the age of the Dongargaon beds as Upper Eocene, but it may be that the remains of *Clupea* have not yet been recognised from the older formations, for the family Clupeidæ dates from the Cretaceous period.

The scales from the infra-trappean bed at Dhamni also belong to the genus *Clupea* and are very similar to the scale found at Dongargaon.

The inter-trappeans at Paharsingha contain small *Lepidosteus* scales, while those at Takli contain a very primitive type of *Nandid* scale. The Nandidæ belong to the Percoid group and presumably are not older than the Tertiary period. Though no fossil remains of the Nandidæ are known, these fishes must have been in existence at a time when there was still a land connection between India, Africa and South America, for their close allies of the family Polycentridæ are found at the present day in West Africa and South America.

The inter-trappean beds at Deothan and Kheri yielded the remains of Teleostean fishes only. Scales of *Clupea* of two types—some with the transverse radii complete and others with the transverse radii widely interrupted—are very abundant; those with complete transverse radii are similar to the one found in the inter-trappean (Lameta ?) at Dongargaon and the infra-trappean at Dhamni.

The most remarkable discovery is, however, the occurrence of the Osteoglossidæ in the Deothan beds. There are 3 fragments of the characteristic scales of this family which I have referred to the fossil genus *Musperia* Sanders (1934) recently described from the old Tertiary formations of Middle Sumatra. Of all the living Teleostean fishes, Osteoglossidæ have a remarkable distribution; they are found in Australia, Indo-Australian Archipelago, Siam, Africa and South America. It has now been recorded, though in a fossil state, for the first time from India. The Osteoglossidæ grow to a large size; *Arapaima* of South America attains a size of 15 feet and is the largest fresh-water fish known. The fossils of the Osteoglossidæ are found in Tertiary formations only.

There is one fragment of a primitive Cyprinid scale of the sub-family Abramadinæ. The Cyprinoids form the most dominant group among the present-day fresh-water fishes, but they do not extend to below the Lower Eocene.

The rest are all Acanthopterygian fishes which are found in great abundance in seas, estuaries and fresh waters not very far from the coasts. Of these, there is one Labyrinthid scale, probably of the family Polyacanthidæ. The Labyrinthid fishes are found in South-eastern Asia and Africa. There are also numerous scales of *Serranus*, *Nandus* and *Pristolepis*, all Percoid fishes of a highly specialised type. The Serranidæ are mostly marine, but a few occur in fresh waters. The Nandidæ, to which the Pristolepidæ are closely allied, are strictly fresh-water forms; they are represented in Africa and South America by allied forms of the family Polycentridæ. Neither of these families is hitherto represented by any fossil form.

Judging from the present-day geographical distribution of the Pristolepidæ and the Polyacanthidæ and from the present-day migratory habits of certain large species of *Clupea*, the Trappean fish-beds were probably laid down after the supposed severance of the land connection between India and Africa in the early tertiaries. The ecological associations of the Lameta and the inter-trappean fish-faunas also point to the same conclusion. When large fishes of the type of *Eoserranus*, *Lepidosteus* and *Pycnodus* flourished in the Peninsula (the age of the infra-trappean bed at Dongargaon) the main river of the area

was probably very large, placid and deep, and its mouth was not very far from Dongargaon. But by the time the inter-trappeans of Deothan and Kheri were laid down, marshy conditions, with lakes and marshes of varying sizes in the neighbourhood of the mouth of a large river, had been established. The conditions then were probably similar to those now prevailing in the lower reaches of the Ganges. The presence of a considerable number of Clupeoid scales of fairly large size clearly indicates the deltaic nature of such a river not very far from the beds mentioned above. Clupeoids are marine fishes but some, like the Shad of America and the Hilsa of India, ascend into large rivers for long distances and give rise to immense, seasonal fisheries. The occurrence of the Nandidæ, the Pristolepidæ, the Polyacanthidæ and the Serranidæ also indicates the maritime nature of the area, for fishes of these families, even at the present day, are commonly met with in fresh waters usually not very far removed from the sea.

Considerable support is lent to the estuarine nature of the fish-fauna of the inter-trappean beds from the discovery of the remains of a genus of palms, *Nepadites* or *Nipa*, in the inter-trappean beds at Chhindwara, a place not very far away from Deothan and Kheri. As is well known, these palms still survive in the Sundarbans and other tropical estuaries. On this point Sahni (1934) observed that:

> "*Nepadites* is not only a genus very characteristic of the Eocene period but, unless these palms have changed their mode of life since then, its occurrence in the northern part of the Deccan indicates the existence of an *estuary*, during the early part of the Inter-trappean period in the proximity of Chhindwara."

Though the geological data about the drainage of the area are obliterated by the overlying traps, still from the very meagre evidence available Mr. H. Crookshank has been able to support my conclusions concerning the habitat of the Deothan fossil fishes. It also appears probable that all inter-trappean beds are probably not of the same age. Judging from the meagre evidence provided by the fish scales, the inter-trappeans of Paharsingha and Takli would seem to be older than those of Deothan and Kheri. Of course, the Lameta beds at Dongargaon are the oldest of all trappean beds from which fish-remains have been studied so far.

From the above it may be concluded that the infra-trappean beds at Dongargaon and the inter-trappean beds at Paharsingha, Takli, Deothan and Kheri were laid down in the early tertiaries, and that there was probably some interval between the deposition of the infra- and the inter-trappean beds during which the change from a predominantly Ganoid to an almost exclusively Teleostean fauna took place. One thing seems to be fairly certain that ecological conditions usually associated with a large and deep river characterised the infra-trappean period, and that by the advent of the inter-trappean period marshy conditions, usually associated with the mouths of large rivers, had set in.

Summary.

The systematic position of the fossil fish-remains from the infra-trappean beds at Dongargaon and from the inter-trappean beds at Takli, Paharsingha, Deothan and Kheri along with their known geological ages are tabulated. The distribution in space and time of the 10 principal types of trappean fishes is discussed, and it is concluded that these beds were probably laid down in the early tertiaries when the lower part of the supposed land connection between India and Africa had already disappeared and when the area occupied by the beds was not very far from the sea coast. It is further pointed out that there was probably sufficient interval between the formation of the infra- and the inter-trappean beds to permit the change from a predominantly Ganoid fauna, comprising *Lepidosteus* and *Pycnodus* of the Lameta beds at Dongargaon, to a fauna of almost exclusively Teleostean fishes, such as the Clupeidæ, the Osteoglossidæ, the Cyprinidæ and a great variety of Acanthopterygians, in the inter-trappeans at Deothan and Kheri.

From an ecological point of view, one thing seems fairly certain that the conditions usually associated with a large and deep river characterised and infra-trappean period, and that by the advent of the inter-trappean period marshy conditions, usually associated with the mouths of large rivers, had set in.

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Clariidæ live in mud in marshy areas of both countries and have thus retained their primitive habits. On account of this we find that *Heterobranchus* and *Clarias*, the two oldest members of the family, are common to the two continents. Tropical Africa with its vast stretches of ancient lakes provided a more suitable *milieu* for these fishes, some of which took to a burrowing mode of life. Consequently they became eel-shaped and their accessory respiratory organs and the associated skeletal elements became degenerate. In India, on the other hand, the conditions were very unstable during the Tertiary period, with the result that the primitive genus *Heterobranchus*, of which fossil remains have been found in the Siwalik formations of the Lower Pliocene, disappeared altogether and only one highly specialised species of *Clarias*,[9] *C. batrachus* Linn., is now found throughout India, while two other less specialised forms, *C. brachysoma* Günther and *C. dayi* Hora, are confined to Ceylon and the Wynaad Hills respectively.

The Bagridæ, like the Schilbeidæ, became established on both the continents at an early date and after the severance of the connection between the two lands evolved independently so that at the present day there is no genus common to the two regions. However, a close parallelism exists between the forms inhabiting similar situations on the two continents. *En passant* it may also be remarked that most of the other Siluroid families of India and Africa are evolved from the Bagridæ.

A remarkable feature of the Schilbeidæ is that no member of the family is found in Ceylon, which may be due to the fact that Ceylon became separated from India at a stage earlier than the disappearance of the land connection between India and Africa. The absence of the Schilbeidæ from Ceylon may also be explained on the assumption that at some period the water courses changed in such a way that in spite of the land connection between India and Ceylon no migration from the north to the south could take place. It is thus seen that unlike the distribution of the land animals, where probably the climatic considerations are of the greatest importance, the aquatic animals are bound within their watersheds and in spite of land connections and favourable climatic conditions between two adjacent lands may not spread from one to the other if their water courses had no chance to become continuous at some period or another. The distribution of fishes, therefore, though extremely important in zoogeographical studies, has thus only a limited value in elucidating the extent of the former land and sea connections.

In this east to west migration of the fauna I have assumed throughout that India was connected with the Far East, at least from the late Cretaceous onwards. This connection was of a very different nature from what it is to-day, for in the early Tertiaries a considerable part of Northern India was under the sea. The Bay of Bengal is considered to be an ancient feature of the physiography of India, so that the old connection between India and the Far East probably stretched over the Peninsula through the coal-field areas of Bengal to the Assam Hills, North Burma and beyond. At certain periods the direct land connection between Assam and Burma was cut off by an arm of the sea, but still Assam remained connected with the Far East through Tibet and Southern China. The distribution of the Indian freshwater fishes affords ample evidence in support of these routes of migration.

I may also refer here to the remarkable similarities between the faunas of the Malay Archipelago, Malabar Zone of South India and Tropical Africa. To account for these anomalies of distribution several workers have been led to establish a southern continent including South America, but of which Madagascar did not form a part. In my opinion when the primitive forms were spreading from Indo-China to Africa they sent branches to the south in all areas over which they passed, and as these southern extremities were away from the main centre of disturbance (the Himalayas) and also somewhat out of the way of the succeeding waves of migration they continued to harbour primitive animals in, what one may say, these corner seats. The islands of the Malay Archipelago, such as Java, Sumatra, Borneo, etc., the Malabar Zone of India and West and South Africa to-day form the limits of the ancient waves of migration and consequently contain many primitive forms, which, owing to the severance of land connections, could not spread any further. Of the genera I have referred to above, *Heterobranchus* of the Clariidæ shows a discontinuous distribution as it is

found in Africa on the one hand and in Banka and Borneo on the other. There is no doubt that even in the Lower Pliocene period its range of distribution must have been more or less continuous, as fossils are known from the Siwalik formations of that period.

It seems highly probable that the southward migration of the Indo-Chinese fauna in the region of the Malay Archipelago must have followed the course of the Indo-Malayan Mountains and of the Malay Arc[5] by a series of river-captures. The strong similarity between the fauna of South India and that of the Malay Archipelago[5] is probably not due to the migrations of the forms *inter se* but to their common origin from an east to west migrating, primitive stock.

In the above discussion I have not taken into consideration the route of migration that now exists between North-western India, through Baluchistan, Persia, Mesopotamia, Palestine, etc., to Africa. This route is known as Jocobi's Arabian region of dispersal and does not seem to have played any important part in the interchange of the freshwater faunas from Africa to India. Some of the Indian forms, however, such as *Glyptothorax* Blyth, *Garra* Hamilton, etc., have undoubtedly spread westwards along this route. *Scaphiodon* Heckel appears to be the only form that may have spread from Persia, Baluchistan and Sind to the Western Ghats.

To sum up it may be stated that the evidence provided by the distribution of the freshwater fishes of India indicates an eastern origin of the fauna and its subsequent dispersal to the west. The close relationship between the Indian and the African freshwater fishes can only be explained on the assumption of a land connection between the two countries. The absence of the Schilbeidæ from Ceylon and their presence in Africa suggests that Ceylon may have become separated from India at a stage earlier than the severance of the land connection between Africa and India. The distribution of freshwater fishes shows that Peninsular India had a land connection with the Far East, at least from late Cretaceous onwards, and probably at no time during this interval it became an island. The similarity in the faunas of South and West Africa, South India and the Malay Archipelago are probably due to the fact that they received branches of the primitive stock when it was migrating from the east to the west along a northern and a considerably more disturbed part of the Oriental region. The above review of the subject clearly shows that there is no African element in the freshwater fish-fauna of India. The existing connection of Africa with North-western India is comparatively of a much more recent date and does not seem to have played any important part in the dispersal of the freshwater faunas.

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ANIMAL ECOLOGY OF TORRENTIAL STREAMS.

BY SUNDER LAL HORA, D.Sc., F.R.S.E., F.N.I.

Animal Ecology of Torrential Streams.*

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ECOLOGY is that branch of biological science which deals with the responses of organisms to the physical and biological factors in their environment. Such responses are popularly known as "adaptations", and for their proper understanding it is of the paramount importance that the structure and the behaviour of an organism should be correlated with the factors in its habitat. Just as an animal organisation is very diversified and thereby we are enabled to recognise genera and species on the nature of certain morphological characters, similarly an environment is composed of a large number of factors, which show an unlimited range of gradations. Adaptation signifies correlation of an animal organisation with its habitat and so long as the varying gradations in a particular environment are not thoroughly understood, the finer adjustments of the animals to their respective external conditions cannot be grasped. In certain cases, where there are marked differences between the habitats of groups of animals generally belonging to distinct genera, or families or to distantly related species, it is easy to indicate that the characters separating one from another are adaptive; but when closely allied species living in an apparently homogeneous environment are studied then it becomes difficult to realize that the minute differences separating them possess any adaptive significance, for though our knowledge of the classsificatiou of species has made great progress, our knowledge of their habits and habitats is very meagre. The fact should not be overlooked that habitats are as difficult to define as are the species.

I have been working on the fauna of Torrential Streams in India for about seventeen years and I confess that it was only when I undertook the study of the Invertebrate fauna, that I became aware of the gradations in this specialized environment. This knowledge has clearly indicated to me the marvellous correlation that exists between the organisation of a torrential animal and its habitat. A field collector usually sweeps the bed of a shallow stream with his bag-net and transfers his catch to a tube containing some alcohol and labels the entire lot "from a clear, rapid-running stream with rocky bed and little vegetation." This material in the hands of museum workers is misleading and suggests that in a single habitat all kinds of forms are met with so that the obvious conclusion is reached that there are no adaptations for particular habitats. For instance a student of mayfly nymphs would find the shrimp-like larvæ of *Bætis* and the disc-like larvæ of Heptageniidæ, such as *Iron*, living together in a hill stream, and unless the conditions under which these two forms live are known it would be difficult to speak of either of the two forms as being adaptive.

Just as the study of an "organism as a whole" is of the greatest value, similarly I would strongly advocate that in all ecological work the environment should be studied as a whole. But there are limitations. In classifying animals we rely on certain "characters" which we consider to be of paramount importance; similarly in the classification of habitats we have to rely on certain "factors" in an environment. Just as importance of "characters" varies with different taxonomists, similarly the importance of environmental "factors" varies with different ecologists. Hubault[1] in his treatment of the invertebrate fauna of the torrents has relied on the oxygen contents and the low temperature of the water, and has attached a secondary rôle to the rate of flow of water. In the course of my work I[2,3] have been impressed by the fact that the swiftness of the current and the nature of the substratum are the main factors and the

* Read at the 25th Meeting of the Indian Science Congress in the Section of Zoology at the discussion on "Amimul Ecology in Relation to India," and published with permission of the Director, Zoological Survey of India.

[1] Hubault, E., "Contribution à l'étude des Invertébrés Torrenticoles," *Bull. Biol. France Belgique. Suppl.*, 1927, **9**, 388.

[2] Hora, S. L., "Ecology, Bionomics and Evolution of the Torrential Fauna, with special reference to the organs of attachment," *Phil. Trans. Roy. Soc., London*, (B), 1930, **218**, 171–282.

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others, though of great value, for the existence of the animals, are themselves in a great measure dependent on the rate of flow of water. To utilise the advantages afforded by the physico-chemical properties of the cool and highly oxygenated waters of brooks, in the first place it is essential that the animals should be able to maintain their hold in swift currents. The following classification has, therefore, been based on the rate of flow of water at different strata and it has been observed that animal organisation shows a definite correlation to this factor in the environment.

A brook consists of a series of rapids, falls and pools, and generally flows over a rocky bed with tufts of mosses and weeds covering rocks and stones here and there. The fauna of the pools is different from that of the rapids and again the animals that live on rocks in a rapid are different from those that live in moss. If there is sand in the bed then we find burrowing animals which are different from the rest. Let us confine our attention to the shallow, rocky part of the stream and here again we must remember that the current at the bottom and sides is much less than that in the centre at a point about three-fifths of the depth from the bottom. We meet with a gradation in the fauna corresponding with the gradation in the flow of the current. Let us select a small portion of the bed in swift current for more thorough investigation. The stones are loosely placed on one another so that interspaces are left between them through which water flows at a considerably slower rate and the current at the bottom among shingles and pebbles is probably negligible. The rock-inhabiting animals of the brooks can thus be divided into 3 strata: (i) those that live on the exposed surfaces of rocks, (ii) those that live in the interspaces and crevices among rocks and stones, and (iii) those that live among shringle at the bottom. Thus according to their positions in the currents the animals are provided with elaborate means of attachment and are correspondingly modified in several ways to offer minimum resistance to the current. The plant-inhabiting animals of the torrents are also of three kinds. Those, like the larvæ of *Tipula*, that live among roots are sheltered from the current and are the least modified for this habitat. Others like the larvæ of *Phalacrocera* and *Nephelopteryx* entangle themselves among plants by means of chitinous processes and lastly the larvæ of *Simulium*, Chironomids, etc., live on plants attached by means of their extremities so that they dangle freely in the current. Though these animals are differently modified for attachment, which is due to the various ways in which they are affected by the current, yet in response to the high percentage of oxygen in the water they have all reduced their gills. The animals of each habitat can be further divided according to the nature of their food. Most members of the torrential fauna feed on algæ and slime covering rocks and stones, but some have evolved highly complicated devices to strain microplanktonic organisms out of the rushing currents and there are few, like the nymphs of *Perla*, which are predaceous.

In broad outline the factors indicated above influence groups of animals and mould them to similar lines. The finer gradations of these very factors distinguish species. Take for example, the three species of *Bætis* described by Dodds[4] from Colorado living on rocks in swift currents.[5] *B. tricaudatus* with three caudal cerci lives in currents flowing at the rate of 5 feet per second. *B. intermedius*, in which the middle caudal circus is decidedly shorter, lives in waters flowing as much as 8 feet per second and finally *B. bicaudatus*, in which the middle circus is represented by a vestige only lives in places where the water flows at the rate of 10 feet per second. The reduction of the middle circus can thus be correlated with the increased swiftness of the current and such a reduction can be traced among the nymphs of other mayflies also. The reduction of the middle circus is accompanied by the tapering of the body posteriorly so that the stream-like moulding of the body is carried to the extreme posterior end. It is clear then that minute difference between species can be correlated with the intensities of certain factors in the environment.

Let us now consider the different body-forms of brook-inhabitants. They are gracefully stream-lined so that the water glides over them smoothly and no "dead water" area or eddy-formation takes place in the neighbourhood of the animal. The animals that swim or swing in the current,

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[4] Dodds, G. S., "Mayflies from Colorado," *Amer. Ent. Soc.*, 1923, **49**, 93–114.

[5] Dodds, G. S., and Hisaw, F. L., "Ecological Studies of Aquatic Insects. I. Adaptations of Mayfly Nymphs to Swift Streams," *Ecology*, 1924, **5**, 137–148.

drical so as to present a stream-line to the current on all sides, whereas those that lie flat on the bottom are stream-lined along the exposed surface and flattened along the opposing surface. The animals either become greatly elongated or they assume limpet-like forms. In the case of the aeroplane struts it has been found that both forms are equally effective in reducing resistance. But it may be asked why some animals assume one form and the others a different form. This differentiation in the ultimate form is due to the initial form with which an organism starts its life in rapid waters, for in nature it seems to be a rule that, with whatever initiative an organism may be endowed in the beginning, it is through the continuous moulding of the same material under different sets of conditions that different forms are produced. New structures do not arise *de novo*, the old structures by taking on new functions are so altered, and consequently alter the entire organisation, that sometimes the genetic affinity between the two allied forms can be hardly discerned.

It is sometimes advanced as an argument against adaptations that similar forms are found in different habitats, but the point to be considered in each case is whether it is adjusted to live or not in the place where it is found. Two different looking dragonfly larvæ are found clinging to plants in swift currents. *Macromia ida*, a flat-bodied larva, belongs to the bottom-dwelling Libellulinæ and *Matrona basilaris*, to the weed-dwelling Calopteryginæ. Both forms being useful for reducing resistance are retained without great change, whereas in response to the pulling action of the current the legs have become elongated and are spidery. The spidery legs enable the animal to swing before the current without losing hold of the substratum. Here is an instance showing divergence in form but convergence in the organs of attachment.

In conclusion, it may be stated that for a proper appreciation of organic evolution or adaptation it is of the greatest importance that the characters of an animal and the factors constituting its habitat should be investigated at the same time, for it is difficult to conceive of a living animal apart from its environment. Ecological studies alone will help us to eliminate all chances of confusion arising out of the similarity of structures under apparently different conditions or of the divergence of characters under apparently identical conditions. My studies have shown that sometimes an identical factor is found in operation under different conditions and *vice versa*.

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ON THE ORIGIN OF THE GREAT RIVER-GORGES OF THE HIMALAYAS, AS EVIDENCED BY THE DISTRIBUTION OF FISHES.

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On the Origin of the Great River-Gorges of the Himalayas, as Evidenced by the Distribution of Fishes.*

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IT is a general feature of the mountain ranges of Asia that they are cut across by rivers which form stupendous gorges. Geographers and Geologists have suggested many explanations of the origin of the great river-gorges, but no one explanation has yet been accepted by all. It is, however, generally recognised that the gorges have been slowly carved by the rivers themselves during the course of ages. Some of the views regarding the origin of the Himalayan gorges are thus summarised by Burrard, Hayden and Heron (1933, p. 261):

"A gorge may be carved by water across a range in many different ways. Firstly, as a new-born range is rising slowly out of the ocean, it may be cut across at intervals by the sea and divided into a series of islands; the channels cut thus in early times may subsequently develop into river-gorges. Secondly, the snow and rain falling on the front slopes of a range may create glaciers and rivers, which slowly cut back by head-erosion and eat through the mountains. Thirdly, the snow and ice accumulating on the crest may gravitate towards the lowest points of the range, and thence flow off in opposite directions and wear away the rock on both flanks simultaneously. Fourthly, a river may be antecedent or older than the mountains, and have maintained its path across the latter as they rose. Fifthly, the flow of a river may be dammed by the rise of mountains across its path, and the waters of the lake so formed may eventually overflow and carve a gorge across the barrier range."

According to the latest paper on the subject by Wager (1937), there are only two alternative theories which are being discussed at the present day to account for the existing drainage pattern of the Himalayas. He states:

"One of the theories postulates that at an early age the Himalaya had ordinary consequent drainage, the rivers flowing north and south from the crest. This simple drainage pattern is considered to have been modified to its present form by some of the south-flowing rivers cutting back through the range and capturing rivers on the Tibetan side. The much greater precipitation on the south side of the range and the much steeper fall and therefore greater erosive power are put forward as possible reasons for the unusual behaviour of the south-flowing rivers. The alternative theory postulates that the Arun and similar rivers always had their present courses which, when they were inaugurated, were the easiest routes down an irregular surface sloping towards the Gangetic plain. Subsequently the Himalayan range is considered to have arisen up across the rivers, but so slowly that by vigorous erosion they were able to keep open their original channels."

The distribution of Himalayan fishes, both on the Tibetan and the Indian sides, sheds considerable light on this controversial problem. Day (1878), Stewart (1909) and the writer (1937) have shown from a comparison of the fish-faunas of the northern and southern faces of the great Himalayan range that the two faunas are very distinct. The writer has also indicated the probable origin of these faunas and concluded that though the Central Asiatic and the Indian faunas are derived from the same source, somewhere in Southern China, possibly Yunnan, the former became differentiated at a somewhat earlier age when the parent stock was of a generalised nature, whereas the fauna of the southren face appears to have been derived from a younger and more vigorous stock which had already become specialised in south-eastern Asia for life in torrential streams. At any rate, there is no indication that the two faunas had a chance to intermingle since their origin and the reason for their isolation is to be looked for in the origin and the present form of the Himalayas.

It is generally recognised that the whole length of the great Himalayan range is of one geological age. There are indications, however, that the Punjab Himalayas arose at a somewhat later date than the other three portions of the range, *viz.*, Assam Himalayas, Nepal Himalayas and Kumaon Himalayas. This would indicate that when the present-day fresh-water fish-fauna migrated from Southern China to India probably in the post-Eocene period, a barrier had already been created between the forms that spread toward north-west and those that spread toward south-west. The distribution of fishes shows that the drainage of the

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Himalayas in the earlier stages was from east to west along both the faces. In the north the Tsangpo probably flowed into the present-day head-waters of the Indus and the combined river thus formed probably drained north-westwards into the Oxus; while in the south the Tertiary "Indobrahm" of Pilgrim (1919) and Pascoe (1919) had a similar course and drained into the Arabian Sea.

It seems that in the beginning the rise of the Himalayan foot-hills was probably of a more or less uniform nature, which permitted the formation of long longitudinal valleys in the foredeeps of the rising range; but later orogenic movements were certainly more marked in some portions of the range than in the others. These differential movements caused the dismemberment of the primary simple drainage pattern, the streams on the northern and the southern faces draining into their respective longitudinal basins. I have indicated in another place (1937*a*) how the distribution of fishes shows the evolution of the present-day sharp hydrographical divisions of the southern face of the Himalayas. A continuous stream of migration of forms like *Garra* Hamilton, *Glyptothorax* Blyth, *Amblyceps* Blyth, *Nangra* Day, etc., was checked by a sharp rise of the sub-Himalayas in the region of the principal peaks of the range near the border of the Assam and the Nepal Himalayas and diverted along the Satpura trend to the Western Ghats and thence to the hills of the Peninsula. Such a route of migration could only explain the occurrence of *Bhavania* Hora (Family: Homalopteridæ), *Parapsilorhynchus* Hora (Family: Cyprinidæ), *Silurus* Linn. (Family: Siluridæ), etc., in the extreme south of India on the one hand and of their close allies, such as *Balitora* Gray (Family: Homalopteridæ), *Psilorhynchus* McClelland (Family: Psilorhynchidæ), *Parasilurus* Bleeker (Family: Siluridæ), etc., in Eastern Himalayas and South-eastrn Asia on the other. In this case we have a clear proof of the sharp rise of the Himalayas not only in the cluster of high peaks found in this region, but in the barrier that was created against the migration of fishes to the western portions of the range and the dismemberment of the mighty river into the Brahmaputra Drainage System and the combined Indo-Gangetic System. Another differential earth movement, probably of a much later date, which elevated the Putwar basin into a plateau (Wadia, 1932) led to the further dismemberment of the "Indobrahm" into the Indus and the Ganges Systems of the present-day drainage pattern of the Himalayas. This division is reflected in the distribution of such genera as *Semiplotus* McClelland, *Chaca* Gray and *Erethistes* Müll. and Trosch., which are common to the Assam Himalayas and the Nepal Himalayas but are absent from the Punjab Himalayas. It is thus seen how a continuous westerly flowing river at the foot of the young Himalayas became dismembered into three drainage systems through sharp, localised orogenic movements. These movements also seem to have affected the drainage on the northern face of the Himalayas and established an easterly-flowing Tsangpo and the westerly-flowing Indus. Some of the changes in the drainage pattern of the Central Asiatic tributaries of the Indus studied by de Terra (1934) may have been contemporaneous with the rise of the Putwar basin or of that of the Pir Panjal.

From the above the following conclusions may be drawn with regard to the evolution of the present-day drainage pattern of the Himalayas, and consequently of the origin of the great river-gorges.

The distinctness of the northern and the southern fish-faunas of the Himalayas definitely favours the view that at an early age the Himalayas had ordinary consequent drainage, the rivers flowing north and south from the crest. Had the Himalayan range risen up across the river so slowly as to enable the rivers to keep open their channels by vigorous erosion there should have been very little difference between the fish-faunas of the *Cis-* and *Trans*-Himalayan portions of such rivers as the Brahmaputra, the Arun, the Sutlej, the Indus, etc. There is every reason to believe, on the other hand, that the rise of the Himalayas was in sharp, sometimes localised, orogenic movements so that the fishes of the southern face of the range were unable to adapt themselves to very turbulent waters and have, even to this day, remained confined along the southern face of the range to low valleys and are rarely found above an elevation of four to five thousand feet.

In this connection it may also be remembered that the so-called Indian monsoon conditions—south-west for four months and

north-east for three or four months—had begun before the Himalayas started to rise, as in the late Cretaceous period open seas of great extent existed to the south of India and some land had been formed to the north. The rise of the Himalayas had a great influence on the distribution of rainfall, for most of the moisture is now precipitated on its southern face; and there is practically no rainfall on the northern face of the Himalayas. Consequently, the rivers along the southern face are very turbulent while those on the northern face are placid, broad-valleyed and deep. Very different sets of ecological conditions were thus produced on the northern and southern faces of the Himalayas and these became accentuated as the mountains rose higher and higher.

When the south-flowing rivers, mainly through their erosive actions, captured the rivers on the Tibetan side it was natural that some of the fishes on the Tibetan side should have been washed down on the southern side, but they had to pass through such precipitous channels before reaching congenial conditions that with the exception of one genus of the Schizothoracinæ—*Oreinus*, a specialised member of the subfamily fully adapted for life in rapid mountain streams—no other member of the Central Asiatic fauna has been able to colonise the southern slopes of the Himalayas.

The migration of torrential fishes along the southern face of the Himalayas and from the Eastern Himalayas to the Hills of the Peninsula shows that the process of river-capture or river-deflection was a fairly common phenomenon in this territory and also in the region of the contiguous hill-ranges to the east. The distribution of specialised hill-stream fishes strongly suggests that in South-eastern Asia, as a rule, the rivers on the west beheaded the rivers on the east (Gregory, 1925) and thus effected the transference of the fish-fauna from the east to the west.

Summary.

A summary of the views regarding the origin of the great river-gorges of the Himalayas is given. It is pointed out that the fish-faunas on the northern and the southern slopes of the Himalayas are quite distinct, and that an explanation of this fact is to be found in the origin and the present form of the Himalayas. The evolution of the present-day drainage pattern of the southern face of the Himalayas is traced from the evidence afforded by the distribution of fishes and it is concluded that the early drainage of the Himalayas was from east to west along both the faces, and that it underwent considerable changes due to differential orogenic movements in the region west of the Tista drainage system and of the Putwar Plateau. The distinctness of the northern and the southern fish-faunas of the Himalayas favours the view that at an early age the Himalayas had ordinary consequent drainage, the rivers flowing north and south of the crest. The distribution of fishes along the southern face indicates that the rise of the Himalayas occurred in sharp, sometimes localised, earth-movements so that the fishes always remained in the valleys and were unable to colonise the precipitous higher reaches. A reference is also made to the influence of the monsoons on the southern face, and to the process of river-captures that probably played a great part in the distribution of fishes from the east to the west.

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NOTES ON THE ZOOGEOGRAPHY OF TIMOR AND SUMBA

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NOTES ON THE ZOOGEOGRAPHY OF TIMOR AND SUMBA

Geologic and oceanographic researches have shown that Sumba and Timor are situated on the same submarine ridge, the so-called outer Banda arc, together with some of the South West Islands, Timorlaut, possibly Kei, Seranlaut, and Seran. This chain of islands is separated by a deep trench from the inner Banda arc, which consists of the island chain, Java-Flores-Wetar-Damar-Banda. The Sumba-Timor-Timorlaut chain is also separated by deep water from the Australo-Papuan Sahul shelf.

These geological facts are of significance to the zoogeographer only if correlated with the data on the distribution of the animal life of these islands. The final aim of such an investigation is to determine *when*, *from where*, and *by what means* every one of the species reached each island. However, such conclusions on the dynamics of animal distribution can be drawn, if at all, only after sufficient descriptive material has been gathered. It is, therefore, the first task of the zoogeographer to determine the place of origin, the faunal history, and the ecological requirements of every species, before he can decide whether or not it needed a land bridge in order to reach a given island. Stresemann (1939) has demonstrated the usefulness of this method in his admirable zoogeographic analysis of the bird fauna of Celebes. I shall attempt to apply similar methods to an analysis of the bird fauna of Timor.

THE FAUNAL COMPONENTS OF THE BIRD FAUNA OF TIMOR

Timor birds can be divided roughly into three groups, a western (Indo-Malayan and Palaearctic), an eastern (Australo-Papuan), and an indeterminate element. However, a close study of the ranges of these species has convinced me that the point of origin of most of them can be determined much more accurately. Stresemann (1939) has shown that nearly all the western species reached Celebes, the Moluccas, and Lesser Sunda Islands on two major invasion routes, one from Burma through Sundaland (Malay Peninsula, Borneo, Sumatra, and Java), and the other from South China through Formosa, the Philippines, and Celebes. Following this suggestion, I have tried whenever possible to divide the western species into these two elements. Likewise the eastern species consist of a Papuan, usually humid tropical, and an Australian, often semi-arid, element. Most Timor species of eastern origin, except some old endemics and some widespread species, can be separated easily into these two components. On the basis of these considerations I have arranged the 137 species of native resident land birds of Timor into the following 15 classes:

1. Endemic, probably of western origin. *Büttikoferella bivittata.*

2. Widespread species of unknown origin. *Dupetor flavicollis, Haliastur indus, Hirundo hitica.*

3. Widespread species, apparently of west origin. *Egretta garzetta, Butorides striatus, Pl leucorodia, Haliaeëtus leucogaster, Falco molu Porphyrio porphyrio, Collocalia esculenta.*

4. Widespread species, probably of east origin. *Poliolimnas cinereus.*

5. Old western element, reached Timor prob ably via Sundaland. *Treron psittacea, Pitta bra chyura, Lalage sueurii, Geokichla peronii, Geokichl dohertyi, Zoothera andromedae, Rhodophila gu turalis, Urosphena subulata, Siphia timore Oriolus viridifuscus, Cinnyris solaris, maugei, Dicrurus bracteatus, Lonchura molu Lonchura quinticolor, Padda fuscata.*

6. Recent western element (either Malaysian o Celebesian). *Podiceps ruficollis, Ardeola Amaurornis phoenicurus, Centropus bengalensi Caprimulgus macrurus, Eurystomus orientali Muscicapula melanoleuca, Lonchura punctulata.*

7. Recent western element (via Malaysia) *Macropygia ruficeps, Streptopelia chinensis, Cucu lus poliocephalus, Tyto alba, Collocalia inexp Anthus novaeseelandiae, Brachypteryx leucophry Pnoepyga pusilla, Cisticola juncidis, Cettia tana, Seicercus montis, Dendrobiastes hypery Lanius schach, Corvus macrorhynchus, sanguinolentum, Piprisoma obsoletum, Ar amandava.*

8. Recent western element (via Philippines Celebes), *Milvus migrans, Hieraaëtus fascia*

xcalfactoria chinensis, *Turnix maculosa*, *Caprinulgus affinis*, *Alcedo atthis*, *Merops philippinus*, *'Iirafra javanica*, *Hirundo striolata*, *Saxicola aprata*, *Cisticola exilis*, *Acrocephalus arundinaceus*.

9. Old western element (via Philippines, Cele-es). *Streptopelia bitorquata*, *Turdus poliocephalus*, *'radypterus montis*, *Phylloscopus* (*trivirgatus*) *'esbytes*, *Cyornis hyacinthina*.

10. Banda Sea element (originally eastern or estern). *Macropygia magna*, *Tanygnathus megarhynchos*, *Coracina novaehollandiae*, *Pseudozosops mülleri*.

11. Secondarily eastern species, of western uperspecies or generic groups (A = Australian, Papuan, AP = Australo-Papuan). *Podiceps noehollandiae* (AP), *Demigretta sacra* (P), *Nycticorax caledonicus* (AP), *Anas superciliosa* (A), *'endrocygna arcuata* (AP), *Aviceda subcristata* P), *Circus assimilis* (A), *Falco longipennis* (A), *ynoicus ypsilophorus* (A), *Irediparra gallinacea* AP), *Rallus philippensis* (P), *Gallinula tenebrosa* AP), *Columba vitiensis* (P), *Merops ornatus* (A), *irundo nigricans* (A).

12. Banda Sea element (of eastern origin). *'tilinopus cinctus*, *Ptilinopus regina*, *Ducula neracea*, *Ducula rosacea*, *Turacoena modesta*, *'allicolumba hoedtii*, *Trichoglossus euteles*, *Trichoglossus iris*, *Chalcites malayanus*, *Halcyon austral-* *Rhipidura rufifrons*, *Monarcha trivirgatus*, *'achycephala orpheus*, *Philemon buceroides*, *Melihaga reticulata*, *Lichmera flavicans*, *Myzomela ulnerata*, *Zosterops montana*, *Zosterops lutea*, *Erythrura tricolor*.

13. Papuan element. *Geoffroyus geoffroyi*, *Eudynamis scolopacea*, *Cacomantis variolosus*, *Halcyon chloris*, *Rhipidura rufiventris*, *Monarcha cinerascens*, *Aplonis minor*.

14. Eastern element (Papuan or Australian). *Phalacrocorax melanoleucus*, *Anas gibberifrons*, *Trichoglossus haematodus*, *Cacatua sulphurea*, *Edolisoma tenuirostre*, *Gerygone inornata*, *Pachycephala pectoralis*.

15. Australian element. *Notophoyx novaehollandiae*, *Accipiter fasciatus*, *Geopelia striata*, *Chalphaps indica*, *Aprosmictus jonquillaceus*, *Ninox eelandiae*, *Megalurus timoriensis*, *Myiagra llis*, *Artamus leucorhynchus*, *Artamus cinereus*, *Sphecotheres viridis*, *Philemon inornatus*, *Licha indistincta*, *Taeniopygia guttata*.

It can be seen from a close study of these 15 classes that I have deviated to a considerble extent from the recently proposed clasifications of Rensch (1936) and Stresemann (1939). Rensch eliminates a high proportion f the fauna from consideration either as g "widespread" or as being a special "Zwischengebietselement." This leaves him among the Timor birds only 54 species (26 western and 28 eastern species), as against 129 species of the above-given classification. Stresemann, in his analysis of the Celebes bird fauna, applies very much the same principles as chosen by me, except that he also leaves a greater number of species unclassified. It seems to me, however, that both authors fail to carry their analysis to the last possible end.

In order to indicate the criteria used to arrive at the above classification, my method will be illustrated by a few examples. Class 3 consists of seven widespread species, apparently of western origin: The genus *Egretta* is widespread in Asia and Africa and even reaches the Americas. Only one subspecies of the species *E. garzetta* reaches the Australian region. *Butorides* is a monotypic genus, but it is widespread in Africa and the Americas, and the pattern of distribution in the Australian region (absence from the Bismarck Archipelago) is proof for the western origin of this species. Similar considerations are true for *Platalea leucorodia*, *Haliaeëtus leucogaster*, *Falco moluccensis*, and *Porphyrio porphyrio*. These four species belong to widespread western groups which reach the Australian region only in a single species or subspecies. *Collocalia esculenta* is the most difficult species of this group to place. Its absence from Australia and from most of Polynesia indicates a western origin. The *linchi* group of Malaysia has all the characters of a primitive group and the eastern *esculenta-leucopygialis* group those of a specialized descendant.

As far as the species in classes 5, 6, and 7 are concerned, there is hardly any other interpretation possible. All are clearly western elements, and if there is any doubt, it is merely on which of the two major invasion routes they reached Timor, via Malay Peninsula-Java, or via Philippines-Celebes. In class 8 those species of the recent western element have been grouped that seem to have reached Timor via Philippines-Celebes. There is no doubt concerning the inclusion in this group of *Excalfactoria chinensis*, *Turnix maculosa*, *Merops philippinus*, *Cisticola exilis*, *Saxicola caprata*, and *Acrocephalus arundinaceus*. Stresemann (1939, p. 325) has already listed these species as users of the

Philippines-Celebes route. The other six species require some discussion. *Milvus migrans affinis* has at the present a range which is widely separated from that of the other subspecies in Asia. The species is entirely absent from the Malay Peninsula, from the Greater Sunda Islands, and from the Philippines, but it is much more probable that this species of savannas and open country passed through the Philippines rather than through the heavily wooded humid tropical Sundaland. The present range of *Milvus migrans* is very much like that of the *Falco tinnunculus-moluccensis-cenchroides* group, and a similar history can be assumed. *Hieraaëtus fasciatus renschi* has a very isolated range on Sumbawa, Timor, Luang, and Wetar. Since this is a species of open, semi-arid country, it is much more likely to have passed through the semi-arid corridor of the Philippines-Celebes route than through Sundaland. We must rely on inferences in these species with wide gaps in their breeding ranges. *Caprimulgus affinis* is so clearly connected with the Asiatic mainland *monticolus* group through intermediate races on Formosa and Luzon that no doubt can exist about the immigration route. This is another case in which an advance in the taxonomy has helped to clear up a zoogeographical problem. The Flores-Timor race of *Alcedo atthis* is nearer to the Celebes race (*hispidoides*) than to the Malayan race (*benghalensis*). This, in conjunction with the fact that the species seems to be absent from Java as a breeding bird, is proof for the use of the Philippines-Celebes route by this species. Even though *Mirafra javanica* and *Hirundo striolata* are absent from Celebes today, there is strong circumstantial evidence that both species used Celebes as stepping stones to reach the Lesser Sunda Islands. They are entirely absent from humid Malaysia and apparently reached Java from the Lesser Sunda Islands, as did *Acrocephalus arundinaceus*, *Cisticola exilis*, *Saxicola caprata*, *Falco moluccensis*, *Caprimulgus affinis*, *Excalfactoria chinensis*, *Merops philippinus*, *Turdus poliocephalus*, and other members of the Philippines-Celebes fauna.

It would lead too far if I were to relate in detail all the evidence which caused me to classify the remaining species of Timor birds in classes 1, 2, 4, 9–15. The criteria were always the same, namely, the geographical distribution of the nearest relatives of each subspecies and a study of the ecological requirements of each species. The position of hypothetical former land bridges was completely disregarded. This is the more possible since there is hardly a spot in the Malay Archipelago which has not been covered by a land bridge by one author or another. I hope I have been able to show that sufficient evidence is available on which to base conclusions, although inferences have to be used wherever the present ranges are discontinuous.

The grouping of the breeding birds of Timor into 15 classes provides the raw material for further analysis. The first question that can be answered is whether ornithologically Timor belongs to the Oriental or to the Australian region. There are 129 species left after eliminating the eight species of the doubtful classes, 1, 2, and 10. Of these the classes 3, 5, 6, 7, 8, and 9 are clearly western, and the classes 4, 12, 13, 14, and 15 are clearly eastern. This adds up to 65 western and 49 eastern species. This leaves the 15 species of class 11 to be classified. There is little doubt that all of them reached Timor from the east, either from Australia or from Papua. Still, they belong so obviously to western (=Oriental or Holarctic) genera or generic groups that they must be considered as having been derived from the Oriental-Holarctic fauna. To include these species with the Australian element of Timor would be a serious zoogeographical error.

The total of the species of the western element on Timor is, therefore, to be increased from 65 to 80 (=62 per cent) as against only 49 (=30 per cent) Australo-Papuan species. On the basis of the composition of its avifauna, Timor is thus to be included in the Oriental region. The analysis of other groups of animals leads to the same conclusion (Rensch, 1936). If the zoogeographic classification of the Timor bird fauna were based on families instead of species and genera, the proportion of the Australian element would be even smaller. Such species as *Chalcites malayanus*, *Eudynamis scolopacea*, *Notophoyx novaehollandiae*, *Accipiter fasciatus*, *Ninox novaeseelandiae*, *Halcyon australasia*, *Halcyon chloris*, *Cacomantis variolosus*, *Edoli-*

soma tenuirostre, *Aplonis minor*, *Megalurus timoriensis*, *Zosterops montana*, *Zosterops lutea*, *Erythrura tricolor*, and *Taeniopygia guttata* would then have to be excluded from the truly Australian element. The colonization of Australo-Papua by Asiatic elements, continuing throughout the Tertiary, makes the decision very difficult as to which species should be considered as "already" Australian and which as "still" Asiatic.

ENDEMISM ON TIMOR

In view of the fact that geologists consider Timor a very old island, the endemism in its avifauna is surprisingly small. There is only a single endemic genus (*Büttikoferella*) which is hardly separable from *Megalurulus* (New Caledonia) and which does not seem very far from *Dumetia*. Among the 137 resident bird species 22 (=16 per cent) are endemic on Timor or in the Timor group, but at least 8 of these are members of more widespread superspecies. The "old" endemism on Timor is thus very small. The subspecific endemism is much greater; there are 67 endemic subspecies on Timor (=47.5 per cent).

The reason for the small number of old endemics on Timor is twofold. One is that in early Pleistocene most of Timor seems to have been submerged, and only the highest mountains remained exposed as small islands in the sea. The fauna of the remaining parts of Timor was completely exterminated at that time. The other reason is that Timor was very insufficiently isolated from the other neighboring island groups and from Australia during late Tertiary and Pleistocene. This facilitated faunal exchange and inhibited the development of endemic forms.

The much younger and much less isolated chain of the Lesser Sunda Islands (from Lombok to Alor) has about 14 good endemic species and a few additional ones which might have to be considered subspecies: *Turnix* (*suscitator*) *powelli*, *Treron floris*, *Otus sylvicola*, *Otus alfredi*, *Halcyon fulgidus*, *Rhipidura* (*rufiventris*) *diluta*, *Rhinomyias oscillans*, *Pericrocotus lansbergi*, *Coracina* (*novaehollandiae*) *floris*, [*Edolisoma* (*morio*) *dohertyi*], *Orthnocichla everetti*, *Pachycephala nudigula*, *Corvus florensis*, *Gracula* (*religiosa*) *venerata*, *Meliphaga lombokia*, *Acmonorhynchus annae*, *Oreosterops superciliosa*, *Oreosterops dohertyi*, and *Pseudozosterops crassirostris*. This number of endemics is not as much smaller than that of Timor as one would expect. Stresemann (1939, p. 313) has recorded some interesting facts on endemism which are worth quoting. On Celebes, for example, there are 84 endemic species among 220 species (=38.2 per cent) and no fewer than 16 endemic genera. On Java, on the other hand, there are 16 (=4.8 per cent) endemic species among 337 breeding species. Of New Caledonia's 68 species, 19 (=27.9 per cent) are endemic, including five endemic genera.

There are 11 endemic species of birds that are restricted to Timor Island (including Semau): *Treron psittacea*, *Rhodophila gutturalis*, *Büttikoferella bivittata*, *Siphia timorensis*, *Sphecotheres viridis*, *Philemon inornatus*, *Meliphaga reticulata*, *Lichmera flavicans*, *Myzomela vulnerata*, *Pseudozosterops mülleri*, and *Padda fuscata*.

It seems zoogeographically justifiable to include among the Timor endemics also those species which have spread to Wetar and the South West Islands. This adds the following 11 species to the list: *Ducula cineracea* (Wetar), *Turacoena modesta* (Wetar), *Gallicolumba hoedtii* (Wetar), *Trichoglossus euteles* (Lomblen to South West Islands), *Trichoglossus iris* (Wetar), *Aprosmictus jonquillaceus* (Wetar), *Geokichla peronii* (Wetar and South West), *Urosphena subulata* (Babar), *Cyornis hyacinthina* (Wetar), *Pachycephala orpheus* (Wetar, Saleyer), and *Oriolus viridifuscus* (Wetar). In view of Timor's greater geological antiquity, it seems justifiable to assume that Timor was the original home of these species.

As original endemics of the Timor group, are possibly also to be regarded *Halcyon australasia* (including Lesser Sunda Islands), *Cinnyris solaris* (west to Sumbawa), and *Erythrura tricolor* (east to Timorlaut), but they have now a fairly wide distribution.

Omitting the three last-mentioned species from our consideration we have 22 species endemic in the Timor group. Among these, *Pseudozosterops mülleri* is hard to place, but of the other 21 species, 12 (=57 per cent) are of eastern origin, and nine of western origin. This figure means that in the old Timor bird fauna, that is, among the earliest colonizers, the eastern element is slightly stronger than the western. Timor was, thus, in pre-Pleisto-

cene, or early Pleistocene, times as accessible to the Australo-Papuan fauna as it was to the Oriental fauna, or even more accessible. The bearing of this fact on Wegener's theory will be discussed subsequently.

The nine western endemics belong to the following above-listed classes: class 1 (*Büttikoferella*), class 5 (*Treron*, *Geokichla*, *Rhodophila*, *Urosphena*, *Siphia*, *Oriolus*, *Padda*), and class 9 (*Cyornis*). Nearly all of these species are either so distinct that the nearest relative cannot be determined, or else they (or the species group to which they belong) are so isolated that it cannot be decided how they reached Timor. It seems more probable that the region of Sundaland rather than Celebes and the Philippines served as stepping stone for most of the species. More knowledge of the position and extent of the pre-Pleistocene islands of the Malay Archipelago is needed before anything further can be stated. The 12 eastern endemics belong to the following classes: nine to class 12 (*Ducula cineracea*, *Turacoena modesta*, *Gallicolumba hoedtii*, *Trichoglossus euteles*, *Trichoglossus iris*, *Pachycephala orpheus*, *Meliphaga reticulata*, *Lichmera flavicans*, *Myzomela vulnerata*), and three to class 15 (*Aprosmictus jonquillaceus*, *Sphecotheres viridis*, *Philemon inornatus*). Since class 12 contains a majority of Papuan elements, it can be concluded that the Papuan element predominates among the eastern endemics. However, it is important to emphasize that the three species of class 15 are of clearly Australian origin and indicate that Timor has been accessible to Australian colonists for a considerable period. All three belong to Australian superspecies.

THE COLONIZATION OF TIMOR BY BIRDS

The raw data tabulated in the preceding section present an opportunity to determine how the various species of birds arrived on Timor. Actually this is only a small portion of the more extensive problem of the colonization of the island belt between the Sunda and Sahul shelves. There is no other region in the world for which so many land bridges have been "constructed" to explain certain distributional phenomena. Rensch (1936) is a typical representative of the school of land bridge "builders." He postulates "a former connection of Timor with Roti-Savu, with Sumba, with Wetar, and with Alor," also "the former existence of a land-bridge between Timor and Timorlaut, which probably included Moa-Babar. . . . We can assume that this connection was interrupted in the most recent past. . . . We can also assume that the Sunda arc was connected with northern Australia by dry land during the recent geological past." In the same manner he connects every island of the Malay Archipelago by land bridges with nearly all other neighboring islands. The Sarasins (1901) and, to a lesser extent, De Beaufort (1926) and other authors, have been equally generous in the postulation of land bridges. It will be shown in a later section that the conception of most of these bridges is based on faulty reasoning, and in particular on an underrating of the natural dispersal faculties of animals. It will be the task of the present section to examine carefully the evidence on which some of these land bridges were established. Stresemann (1939) has already shown that land bridges to Java and to Saleyer-Flores are not needed to explain the colonization of Celebes by birds. It seems that the time has come to reëxamine closely all the previously proposed land bridges in the light of the new facts on passive chance dispersal. I am afraid very few of these bridges will stand up under such a critical analysis. Hypothetical bridges in the Malay Archipelago that I am sure will not survive are: (1) the Flores-Saleyer-Celebes bridge, (2) the Alor-Timor bridge, (3) the Sumba-Timor bridge, (4) the Wetar-Timor bridge, (5) the Timor-Australia bridge, (6) the Babar-Damar bridge (in fact, any bridge between the inner and the outer Banda arc), (7) the Kei-Aru bridge, (8) the Seran-New Guinea bridge, (9) the Seran-Buru bridge, (10) the North Moluccas-Seran bridge, and (11) the Sula-Buru bridge.

It would lead too far in the present paper to test the validity of all these land bridges. I shall limit myself to an analysis of only those bridges that were proposed by Rensch to explain the composition of the Timor fauna. Such an analysis will have to be preliminary, since the time has not yet come to include a full evaluation of ecological factors. Not all faunal differences can be expressed

entirely in terms of geographical accessibility, a point which is well illustrated by the faunal difference between humid western and dry eastern Java. A low island like Sumba cannot have a mountain fauna, and it will always differ in this respect from a mountainous island, even if the two had been connected recently by a land bridge. Furthermore, there are always random faunal differences between distant localities, even though they may be permanently connected. The ecological and historical factors that cause such differences are frequently obscure. It is obvious for the reasons just mentioned that all zoogeographic interpretations should be treated with some caution.

Timor and Sumba

The islands of Sumba and Timor are situated on the same geanticline and of all the possible land bridges leading to and from Timor, the Sumba-Timor bridge has the best geological basis. A drop of the sea level by 1160 meters (or a rise of the island chain by the same amount) would establish a complete dry land connection between the two islands. The distance between Timor and Sumba is about 300 kilometers, but Roti and Savu Islands narrow the gap and serve as possible stepping stones, reducing the largest jumps to less than 100 kilometers in Savu Strait and to 75 kilometers in Dao Strait.

A comparison of the avifaunas of the two islands yields the following facts. Eighty-one (=59.2 per cent) of the 137 species of breeding birds of Timor occur also on Sumba. This suggests a rather close relationship of the two faunas, but actually 77 of these species are widespread and are common residents on one or several of the islands of the Lombok-Alor group of the parallel chain of the Lesser Sunda Islands. The four exceptions are the following:

1. *Dendrocygna arcuata:* A species widespread west, north, and east of the Lesser Sunda Islands. It occurs on Java and Bali on the inner Banda arc, and has been able to colonize New Caledonia, Fiji, and other oceanic islands. The species may yet be found on the Lombok-Alor chain. At any rate, such a widespread species cannot be listed as evidence for a Sumba-Timor bridge.

2. *Circus assimilis:* Amadon (1941, Emu, vol. 40, pp. 372–375) has shown that Sumba-Timor birds belong to the north Australian race *rogersi.* The species has also jumped across to Celebes. Rensch (1931) suggests that the species is only a non-breeding visitor to Sumba and Timor, but it is likely that it is still to be found on Wetar, Alor, or other islands in the grassland belt. The total range of the genus *Circus* makes it seem possible that Celebes is the point of origin of the species *assimilis* and that it has spread from there via Lesser Sunda Islands to Australia rather than vice versa. The wide distribution of the species *assimilis* indicates that the absence on the Lombok-Alor group is insignificant.

3. *Megalurus timoriensis:* The species (map, see Stresemann, 1939, Jour. Ornith., vol. 87, p. 344) has a distribution very much like *Circus assimilis,* except that it settled also on Amboina and in the New Guinea area. The Sumba race *inquirendus* is closer to the Australian race *alisteri* than to the Timor population. This indicates independent colonization from Australia. *Turnix everetti* (Sumba), a descendant of *T. pyrrhothorax* (Australia), is another case of an Australian colonization of Sumba, independent of Timor. A third one is found in the genus *Myzomela.* The Sumba form *dammermani* is a subspecies of the Australian species *erythrocephala,* while Timor is inhabited by *Myzomela vulnerata,* which is related to the Banda group of *annabellae, boiei, batjanensis, chloroptera,* etc. None of the three cases (*Megalurus, Turnix,* and *Myzomela*) supports a former land connection between Sumba and Timor.

4. *Artamus cinereus:* A species widespread in the Timor group (Semau, Timor, Letti, Sermatta), but apparently found only once on Sumba. Since it has not been found by Doherty, Everett, Dammerman, or Stein, it is possibly listed from Sumba by mistake. Its colonization of Timor from Australia proves the ability of this species to jump water barriers, and it would not be unexpected to see the species continue its spread to Sumba. Such a spread, however, requires no land connection.

This analysis shows that the assumption of a Sumba-Timor land bridge is not required to explain the distribution of a single species of birds. On the contrary, the faunal relation-

ships of each of these two islands of the outer Banda arc are with its nearest neighbor on the inner Banda arc, Timor with Wetar and Sumba with Flores, from which they are separated by deep sea trenches (for details, see below). This distribution pattern is in conflict with the land bridge theory but is in excellent agreement with the hypothesis of chance dispersal across water gaps.

Timor and Wetar

The bird fauna of Wetar is probably still insufficiently known, since only about 80 breeding species are known. The previous explorers (Hoedt, Riedel, Schädler, and Kühn) were faced by many difficulties, and no bird collection has been made since 1902. The mountains are not only lower (they rise to only 1500 meters) but also more arid than those of Timor; in fact, Wetar seems to be one of the driest islands of the Sunda arc. Aridity, lack of high mountains, and geologically young age (most of Wetar is volcanic) combined account for the small number of breeding species. Those that are present are Timor elements. Aside from *Megapodius* and *Falco peregrinus*, which may yet be discovered on Timor, Wetar has only a single species of bird (*Otus scops tempestatis*) of which a geographical representative is not found on Timor. The Wetar bird fauna can thus be described as poorer than that of Timor (only 57 per cent as many species) but otherwise practically identical with it.

This is a purely zoogeographic identity. Taxonomically there is a considerable degree of difference between many of the geographical representatives on the two islands. In fact in two species pairs, *Myzomela vulnerata* (Timor) and *kuehni* (Wetar), and *Lichmera flavicans* (Timor) and *notabilis* (Wetar), the difference is so striking that perhaps no immediate relationship exists. *Sphecotheres hypoleucus* (Wetar) is a good species but clearly a geographical representative of *S. viridis* (Timor). In 18 species the Wetar subspecies is different from the Timor form; this includes such typical members of the Timor fauna as *Ducula cineracea*, *Turacoena modesta*, *Trichoglossus iris*, *Aprosmictus jonquillaceus*, *Cyornis hyacinthina*, and *Oriolus viridifuscus*, six species which are restricted to Timor and Wetar and are not found anywhere else in the South West Islands or Lesser Sunda Islands.

How is the faunal relationship of the two islands to be interpreted? The distance between Wetar and Timor is merely 50 kilometers; in fact, if Kambing Island, which lies between them, has served as a stepping stone, the width of the greatest gap is reduced to 25 kilometers. In contrast to these very favorable conditions for transoceanic dispersal is the configuration of the ocean bottom. There is a deep trench between Timor and Wetar which reaches a depth of more than 2000 meters between Kambing and Timor and of more than 3000 meters between Wetar and Timor. This is surely not the place to look for a land bridge. The extreme similarity of the Wetar fauna to that of Timor, together with the well-developed endemism on Wetar, indicates to me that Wetar is a fairly old island which has always been in close proximity to Timor. There is no need for a land bridge which would be in conflict with the geological findings.

Timor and the South West Islands

The faunal relationship between Timor and the South West Islands (other than Wetar) is simple to describe. These islands have a typical, but badly depleted, Timor fauna, lacking most of the endemics of the Timor group. The fauna is mainly composed of widespread elements. Very important is the point that neighboring islands are faunally most closely related, whether they are on the inner or on the outer Banda arc. Thus the fauna of Damar is closer to that of Babar than to that of Roma. Kisser, which is not connected with either arc, has a fauna which is similar to that of the neighboring island of Letti on the outer Banda arc.

On the islands that are nearer to Timorlaut, a slight Timorlaut element is noticeable. This consists of the following species and subspecies (D = Damar, B = Babar): *Accipiter novaehollandiae polionotus* (D), *Rallina tricolor victa* (D), *Ducula concinna* (B, D), *Ptilinopus wallacei* (B), *Tanygnathus megalorhynchos subaffinis* (B), *Pitta brachyura vigorsii* (B, D), *Edolisoma tenuirostre dispar* (D, Roma), *Monarcha (Heteranax) mundus* (B, D), *Myzomela boiei annabellae* (B), and *Aplonis metallica circumscripta* (D). The mo peculiar bird of the South West Islands is the

endemic genus *Dammeria henrici*, restricted to Damar, the relationship of which is still obscure but which is apparently close to, if not congeneric with, *Dendrobiastes*.

All the species which are found on the South West Islands are excellent transoceanic colonizers. There is no evidence in the fauna of the South West Islands of a land connection either with Timor or with Timorlaut and the Moluccas. It is interesting to note that the inner chain of islands (Roma, Damar) has as high or higher a Papuan admixture than the outer chain (Letti-Babar). The faunal composition of each of these islands is determined by the availability of the source of immigration and not by the course of the submarine mountain ridges on which it is situated.

Timor and Celebes

It has never been claimed that Timor and Celebes were ever directly connected by a land bridge which did not include any other islands of the region. This is an obvious impossibility, since Flores is directly in the path of such a connection, and Flores has, therefore, been included in the Timor-Celebes land bridge by those who favor such a connection. The weakest part of this bridge is that between Flores and Celebes. Rensch (1936) lists among birds, *Tanygnathus megalorhynchos*, *Loriculus flosculus*, and *Phylloscopus presbytes*, as proofs for such a bridge. However, each one of these three species has a different distributional history, and all three (or the genera to which they belong) are well known for their ability to spread from island to island. Rensch also quotes the distribution of the genera *Monachalcyon* and *Myza* as proof for a Flores-Celebes bridge, but this claim is based on faulty taxonomy (both genera *sensu* Rensch are artificial). It is for these and other reasons that Stresemann (1939, p. 338) rejects a Celebes-Flores land bridge. He points out that the faunas of the Lesser Sunda Islands and of south Celebes are much too different and, furthermore, that the fauna of the intervening Kalao group does not indicate any former continental connection with Celebes. I agree entirely with this conclusion. He then analyzes the list of species which colonized Celebes from the Lesser Sunda Islands and vice versa (*ibid.*, pp. 318, 325) and comes to the conclusion that this colonization must have been very recent because all these species are racially identical on both sides of Flores Sea, or at least only very slightly differentiated. This is true for the species listed by Stresemann, but I notice that he omits from his list the five species of my class 9 of Timor birds [*Streptopelia bitorquata*, *Turdus poliocephalus*, *Bradypterus montis*, *Phylloscopus* (*trivirgatus*) *presbytes*, and *Cyornis hyacinthinus*]. Admittedly, the immigration route Philippines-Celebes-Lesser Sunda Islands is not proved for some of these species, but it is more probable than any other. It is certain for *Turdus* and for *Phylloscopus*, but even though both of these species are mountain birds, they cannot be considered proof for a land bridge. *Turdus poliocephalus* is a notable transoceanic colonizer, and *Phylloscopus* (*trivirgatus*) has been able to reach San Cristobal as well as such isolated places as Biak and San Matthias. Neither species requires land bridges to explain its present range. This is even more true for the more recent element (classes 6 and 8 of my tabulation). All the species contained in these classes indicate by wide ranges and by their occurrence on many oceanic islands that they have no difficulties in overcoming water gaps. Significant is the point, emphasized by Stresemann, that ecological factors have been most important in determining what species crossed Flores Sea (from Celebes to the Sunda chain and vice versa). All the species of class 8 are inhabitants of grasslands or of the open country in the lowlands. The same is true for nearly all of the species of class 6. It can thus be stated that, at least among birds, the ecological requirements of a species are as important in determining whether it can cross from one island to the next, as the presence or absence of land bridges. In the more or less arid zone of southern Celebes and the Lesser Sunda Islands, birds of arid habitats are the most successful transoceanic colonizers.

Timor and Australia

Wallace, in his "Malay Archipelago," notes that Timor is separated from Australia by nearly 300 miles of open sea, while it is connected with Java and the other Sunda Islands by an unbroken chain of islands,

separated from one another merely by narrow straits. He states that it is, therefore, surprising that the Australian element is almost as strong on Timor as the Oriental fauna, and explains it as follows: "To account for the present state of things, we should naturally suppose that Australia was once much more closely connected with Timor than it is at present, and that this was the case is rendered highly probable by the fact of a submarine bank extending along all the north and west coast of Australia, and at one place approaching within twenty miles of the coast of Timor. This indicates a recent subsidence of North Australia, which probably once extended as far as the edge of this bank, between which and Timor there is an unfathomed depth of ocean.

"I do not think that Timor was ever actually connected with Australia, because such a large number of very abundant and characteristic groups of Australian birds are quite absent and not a single Australian mammal has entered Timor; which would certainly not have been the case had the land been actually united. . . . Neither do any of the most characteristic groups of Australian insects occur in Timor, so that everything combines to indicate that a strait of the sea has always separated it from Australia, but that at one period this strait was reduced to a width of about 20 miles."

My own conclusions are in substantial agreement with those of Wallace, published almost 75 years ago (1869). The former proximity of Timor and Australia, which Wallace postulated to explain the similarities of the faunas, has been substantiated in the meantime by geologists. It was the lowering of the ocean level during the Pleistocene glaciation that exposed the shallow Sahul shelf and reduced the width of Timor Strait from 300 to 45 miles. This gap of about 45 miles, however, never disappeared entirely. All the zoogeographic facts contradict, as Wallace states correctly, the existence of a former land connection with Australia. The few authors, like Rensch (1936, p. 191), who believe in such a land bridge, vastly underrate the dispersal faculties of the animals that have passed from Australia to Timor or vice versa.

Stresemann (1939) has pointed out recently that Timor was an important stepping stone during the Pleistocene faunal "migration" along the Asia-Philippines-Celebes-Flores-Timor-Australia grassland corridor. I am discussing this phenomenon in more detail in a different publication (Mayr, in press), but I might mention that at least the following species of birds seem to have reached Australia via this stepping stone: *Milvus migrans*, *Falco cenchroides*, *Excalfactoria chinensis*, *Ptilinopus cinctus*, *Macropygia phasianella*, *Cacomantis variolosus*, *Eudynamis scolopacea*, *Tyto alba*, *Tyto longimembris*, *Halcyon sancta*, *Eurystomus orientalis*, *Pitta brachyura*, *Mirafra javanica*, *Coracina novaehollandiae*, *Lalage sueurii*, *Anthus novaeseelandiae*, *Cisticola exilis*, *Cisticola juncidis*, *Acrocephalus arundinaceus*, *Rhipidura rufifrons*, and *Oriolus sagittatus*.

This list is, of course, only a minimum number. It does not include all the widespread herons, like *Ardea sumatrana*, *Egretta garzetta*, *E. intermedia*, *Cosmerodius albus*, *Demigretta sacra*, *Butorides striatus*, *Ixobrychus minutus*, *Botaurus poeciloptilus*, etc., which might have reached Australia via Timor, but for which the evidence is not conclusive. It would be easy to compile similar lists for hawks, ducks, rails, and many other orders and families. The importance of Timor for the colonization of Australia by avian immigrants has, up to the present, been considerably underrated.

Among the 137 species of breeding birds of Timor no fewer than 76 (=55.5 per cent) occur also in Australia or are represented by a member of the same superspecies. For 61 species, however, Timor Strait is an effective distributional barrier. This group includes primarily inhabitants of mountain or monsoon forest, for which the ecological conditions in northwestern Australia are not suitable, for example, *Pnoepyga*, *Geokichla*, *Zoothera*, *Turdus*, *Brachypteryx*, *Urosphena*, *Horeites*, *Phylloscopus*, and many others. However, this class contains also a few inhabitants of grasslands or open country which should have been able to reach Australia. This is true for *Hirundo striolata*, *Rhodophila gutturalis*, *Saxicola caprata*, *Lanius schach*, *Amandava amandava*, *Pao fuscata*, *Lonchura quinticolor*, *L. punctulata*, and *L. molucca*. It is not clear whether it accident or some special ecological require

ments which have prevented these species from reaching Australia.

In contrast with the species which reached Australia via Timor are the 14 species of class 15, which came to Timor from Australia, and the 22 species of classes 11 and 14, of which at least some came from Australia. The Pleistocene proximity to Australia has thus influenced the composition of the Timor fauna considerably, although not quite so much as indicated by Wallace, who seems to have underestimated the Papuan and Banda Sea element.

SUMMARY OF THE ZOOGEOGRAPHY OF TIMOR

I can do no better than to introduce my summary on the zoogeographic position of Timor with a quotation from Wallace (1869): "I have dwelt at some length on the origin of the Timorese fauna, because it appears to me a most interesting and instructive problem. It is very seldom that we can trace the animals of a district so clearly as we can in this case, to two definite sources [Asia and Australo-Papua]; and still more rarely that they furnish such decisive evidence of the time, and the manner, and the proportions of their introduction. We have here a group of Oceanic Islands in miniature—islands which have never formed part of the adjacent lands, although so closely approaching them; and their productions have the characteristics of some Oceanic Islands. . . . It has been objected to Mr. Darwin's theory,—of Oceanic Islands having never been connected with the mainland,—that this would imply that their animal population was a matter of chance; it has been termed the 'flotsam and jetsam theory.' . . . But in the case which I have here described, we have the most positive evidence that such *has* been the mode of peopling the islands. Their productions *are* of that miscellaneous character which we should expect from such an origin."

There is little that can be added to this masterful analysis by the pioneer of the science of zoogeography. Many land bridges have been proposed since Wallace to account for the present composition of the animal life of Timor, but, as I believe I have shown above, a careful analysis does not support a single one of them. This is true for birds, and I am confident that it will be confirmed for other animals as soon as proper criteria are applied.

1. Of the 137 species of breeding land birds of Timor Island, eight are of uncertain origin. Of the remaining species, 65 (=50.4 per cent) came from the west, and 64 species came from Australo-Papua. If the eastern species of western genera are added to the western element, its percentage rises to 62 per cent. Timor must, therefore, be included with the Oriental region.

2. Timor lies on the same submarine bank as Sumba, Timorlaut, and Seran, but is separated from Wetar by a deep channel. Faunistically, or at least ornithologically, it is most closely related to Wetar.

3. The drying up of most of Sahul shelf at the height of Pleistocene glaciation narrowed the width of Timor Strait from 300 miles to 45 miles and facilitated a considerable faunal exchange between Australia and the Malay Archipelago, with Timor serving as stepping stone.

THE ZOOGEOGRAPHY OF THE SUMBA BIRD FAUNA

The composition of the bird fauna of Sumba reflects very accurately both the geographical position and the ecological conditions of this island. Being situated merely 40 kilometers south of Flores, it has on the main a fauna which is very similar to that of Flores. But being much more arid and without high elevation, it lacks all the species that are restricted to rain or to mountain forest. As a consequence, its bird fauna is much poorer than that of Flores, consisting of only 103 species as against 140 species of breeding land birds in Flores.

ENDEMISM

The endemism on Sumba is very slight. No genus of birds is endemic; there are eight endemic species and 26 endemic subspecies, a

total of 34 endemic forms, which is 33 per cent of the bird fauna. These are the endemic species: *Turnix everetti*, *Treron teysmanii*, *Ptilinopus dohertyi*, *Rhyticeros everetti*, *Siphia harterti*, *Rhinomyias stresemanni*, *Cinnyris buettikoferi*, and *Dicaeum wilhelminae*. However, seven of these are clearly geographical representatives of other species, and most of them could almost equally well be considered subspecies. *Siphia harterti* is the only endemic species on Sumba which is not member of a more widespread superspecies, and even this species is evidently related to *Siphia timoriensis* and *S. dumetoria*. This lack of pronounced endemism indicates either that Sumba is a young island, or that it has had a continued active faunal exchange with neighboring islands, or both.

THE ORIGIN OF THE SUMBA AVIFAUNA

Nearly all the 103 species of breeding Sumba birds are also represented on the Lombok-Alor chain and can be considered as having been derived from there. The only exceptions are the following species: (1) *Dendrocygna arcuata*, (2) *Circus assimilis*, (3) *Turnix everetti*, (4) *Larius roratus*, (5) *Rhyticeros everetti*, (6) *Megalurus timoriensis*, (7) *Muscicapa* (*latirostris*) *segregata*, (8) *Artamus cinereus*, and (9) *Myzomela erythrocephala*. These nine species illustrate the flotsam-jetsam principle very nicely. Specie 1 is probably still to be recorded from the Lesser Sunda chain. Species 2, 3, 6, and seem to have immigrated directly from Australia (see p. 176). Species 4 and 5 seem to have come from the Moluccas, species 8 fror Timor, and species 7 from the Palaearctic. The faunal composition of Sumba makes it unnecessary to postulate any land bridge. Rensch (1936) quotes *Tanygnathus megalorhynchos*, *Rhinomyias*, *Culicicapa*, and *Ac monorhynchus annae* as proof for a former Flores-Sumba bridge. He overlooks the fac that each of these species has a different faunal history. The only joint attribute of these four species is that they do not occur on any of the other Lesser Sunda Islands. If the 103 breeding species are divided into eastern and western species, the following composition of the bird fauna is found: 57 species are western (56.5 per cent), 44 specie are eastern (43.5 per cent), while two are uncertain. Sumba clearly belongs to the Orient region.

REGIONAL ZOOGEOGRAPHY, LAND BRIDGES, AND DISPERSAL FACULTIES

The zoogeographers of island regions belong to two rather well-defined schools. The one, which I like to call (with a bit of humor) the "naive" school, takes it for granted that two islands or other disconnected land masses must have been united previously by a land bridge if parts of their faunas of flightless animals are identical or closely related. This concept provided a great stimulus to faunistic research, since it implied that a careful analysis of faunal differences and relationships would permit the reconstruction of palaeogeographic maps showing the distribution of land and sea in former ages. Conversely, it was assumed that a knowledge of former land connections, as provided by geology, would explain the phenomena of present distribution.

In recent years an ever increasing body of facts has accumulated proving that this simple hypothesis is not correct. In this, geologists and biologists have cooperated. Land bridges are now readily admitted only for such islands as Britain, the Greater Sunda Islands, the Aru Islands, and Formosa, whic prove by their well-balanced faunas that they once must have been part of a continent. The zoogeographical evidence is well supporte by geological data in all the cases mentioned. However, the existence of former land bridge must be questioned in the case of all islands with an impoverished or unbalanced fauna. These new findings and interpretations effected a considerable change of opinion among zoogeographers; in fact they resulted in the development of a new school. The proponent of this school of zoogeography point out that the dispersal faculties of island animals have been vastly underrated in the past (Gulick, 1932; Darlington, 1938; Mayr, 1941; Zimmerman, 1942). This is true not only of flying animals, like bats, birds, and most insects, but of nearly all groups. There is ample evidenc that even Anura and true fresh-water fish

occasionally overcome ocean gaps. It has been found that even strictly oceanic islands in the Pacific may have rather rich faunas of snails, flightless insects, lizards, and other animals which were formerly believed to be able to spread only with help of land bridges. The geological evidence against land bridges is so unequivocal and convincing in these instances that no doubt remains that these species must have been deposited on these islands by hurricanes or marine currents or by any other means except land bridges. If gaps of 2000 and 3000 kilometers can be spanned, how much more potent must be the factor of passive dispersal where gaps of only 20 or 100 kilometers are involved! The importance of rafts for this dispersal has been stressed by Matthew (1915), M. A. Smith (1943), and others. Dispersal through the air seems to be even more important, particularly for those organisms and their eggs which are unable to withstand long exposure to salt water.

Birds, bats, and Lepidoptera, being flying animals, have always been credited with a considerable ability to cross water barriers. However, it has been pointed out by Stresemann (1927–1934, 1939), by Rensch (1936), by Mayr (1941), and others that birds, for example, are as useful as zoogeographic indicators as are strictly terrestrial groups. The most successful colonizers among the beetle fauna of eastern Polynesia are small flightless species that breed in dead twigs. Some of the small species of land snails seem to be particularly adapted to inter-island transport. The factors that promote such colonization, like rafts and hurricanes, have been discussed by so many recent authors (Gulick, 1932; Darlington, 1938; Zimmerman, 1942) that nothing more needs to be said.

Why certain species and genera are so successful in overcoming water barriers and others are not, is a point about which we require considerably more information. The relative dispersal faculty of various bird species and genera has been discussed by me repeatedly (Mayr and de Schauensee, 1939; Mayr, 1941). Nearly all the species that are found in the Malay Archipelago in the island belt between Sunda and Sahul shelves are good colonizers. Parrots, pigeons, honeyeaters, starlings, and white-eyes have been particularly successful colonizers in Polynesia, and the reason seems to be that they all travel occasionally in flocks. If such a flock is blown out to sea, it has an infinitely better chance of establishing itself on a previously unoccupied island than a single individual. Woodpeckers, on the other hand, are among the most solitary of the birds. This may account for the fact that they have made so little progress in colonizing the Malay Archipelago. They got into the Philippines, two species reached Celebes, and one the Lesser Sunda Islands (east to Alor). This compares with 18 species on Borneo and more than 20 on Sumatra.

Mammals are, on the whole, poor colonizers of islands. Simpson (1940a) points out how few successful colonizations of Madagascar and the West Indian Islands have been made. The very impoverished mammal fauna of Celebes and of the Lesser Sunda Islands shows that the same is true of the Malay Archipelago. The factors that control the distribution of a particular genus are often rather complex. The marsupials of the genus *Phalanger* have unusually well-developed dispersal faculties. They reached the Solomon Islands, the Admiralty Islands, the Timor group, the Moluccas, and Celebes. Yet they have been unable to jump the small gap between Celebes and Borneo. It seems likely to me that this gap was actually bridged repeatedly, but that the numerous predators on Borneo have prevented the establishment of *Phalanger*.

The fact that even mammals can cross water gaps is demonstrated particularly well by the mammals of the Kei Islands. A land bridge between the Kei Islands and New Guinea has frequently been postulated because there are six species of marsupials on the Kei Islands. They are:

1. *Phalanger orientalis:* This is an extremely successful colonizer which has spread from western New Guinea to the Kei Islands, to Timor and Wetar, to the Moluccas. Offshoots of it have even reached the Celebes group (*celebensis*) and the Solomon Islands (*breviceps*). The population from western New Guinea, the Kei Islands, the southern Moluccas (Buru and Amboina), and the Timor group (Timor, Wetar) has not yet broken up into distinct subspecies. This in-

dicates the recent date of much of this colonization.

2. *Phalanger maculatus:* Also a highly successful over-the-water colonist, which has managed to get even to the well-isolated Admiralty Islands. It is widespread in the Moluccas and has reached even the Celebes group. There is little subspecific differentiation over most of the range of the species.

3. *Petaurus papuanus:* The little flying phalanger has spread from the New Guinea area to New Britain, the Kei Islands, and northern Moluccas. This range indicates over-the-sea dispersal but does not actually prove it. Still, the species cannot be taken as proof for a former land bridge. The same is true for the fourth species.

4. *Echymipera doreyana:* Known only from islands on the New Guinea shelf and from the Kei Islands.

5. *Thylogale brunii brunii:* Known from the Aru and Kei Islands, while, according to Tate and Archbold (1937, Bull. Amer. Mus. Nat. Hist., vol. 73, p. 415), *Th. b. lauterbachi* is the race of southern New Guinea. The fact that south New Guinea and the Aru Islands have different subspecies, even though they were connected by land only some 10,000 to 20,000 years ago, while the same subspecies occurs on the Aru and Kei Islands, which are separated by an oceanic deep, indicates clearly that *Th. brunii* must have been carried by an oceanic current from Aru to Kei. This colonization must have taken place very recently, since the Kei Island population has not yet developed into a separate race.

6. *Dendrolagus ursinus keiensis:* The Kei Islands are the only place off the Australo-Papuan shelf where a *Dendrolagus* occurs.

The Kei Islands, with six species, have a very poor marsupial fauna, compared to New Guinea with 50 to 100 species. However, the Kei Islands fauna is rich compared to that of Halmahera (only *Phalanger* and *Petaurus*) and the southern Moluccas (only *Phalanger* and the endemic *Rhynchomeles prattorum*). Noticeable also is the slight degree of endemism among the six species of Kei Islands marsupials. The answer is presumably ecological. The Kei Islands are only 100 kilometers distant from the shore of Pleistocene Sahul-land and near the place where the large rivers that drain the Snow Mountains must have entered the sea. These rivers, which probably compared favorably in size with present-day Fly, Sepik, and Mamberano rivers, must have been a great source of tree rafts, and this may be an explanation for the rich mammalian fauna of the Kei Islands. Halmahera and Seran, on the other hand, although they are in distance closer to New Guinea, are situated opposite a mountainous coast, along which only small streams enter the sea. There was much less opportunity for colonization by rafts.

Some additional evidence regarding a land bridge between the Kei Islands and New Guinea can thus be summarized as follows: All the geological data are in conflict with the theory of a former land bridge (at least during geologically recent times). The composition of the fresh-water fish fauna is also opposed to such an explanation. There is not a single primary fresh-water fish to be found on Kei, and the secondary fresh-water fish show a greater affinity with the Indian than with the Australian fauna. It is for all these reasons that it is to be concluded that no late Tertiary or Pleistocene land bridge existed between Aru and Kei Islands and that the six species of marsupials reached the Kei Islands on rafts. The slight or absent racial differentiation indicates that this colonization took place quite recently, possibly while the edge of Sahul shelf was near the Kei Islands during the height of the Pleistocene glaciations.

Different dispersal factors must be taken into consideration for each island and for each group of animals. It is quite possible, for example, that it will be shown eventually by comparative studies that the Kei Islands have a particularly high Papuan element in all groups that depend on rafts for dispersal, while Halmahera has a particularly high Papuan element in the groups that are carried through the air. More faunistic and taxonomic work needs, however, to be done before such studies can be undertaken.

Amphibians are another group of animals which are frequently considered as incontrovertible proof of former land bridges. This also has become very doubtful in recent years. Most amphibians, whether as eggs, larvae, or adults, are very susceptible to injury by salt

water. It is improbable that they would survive lengthy oceanic voyages on rafts. Therefore, if frogs are found on islands with otherwise oceanic faunas, like the Fijis or the Caribbean Islands, one must assume that they were transported there by hurricanes, clinging to palm fronds or other wind-borne vegetation. In the island region of the Malay Archipelago the species of the arboreal genus *Rhacophorus* (in particular *leucomystax*) have a much wider distribution than the terrestial, i.e., aquatic, species. Of about 35 species of Java frogs and toads, only nine or ten reached Lombok, and only two Timor. For most frogs even narrow ocean straits are dispersal barriers of considerable magnitude; still, the Australian species *Hyla rubella* managed to reach both Timor and Timorlaut. These fragmentary notes are offered merely because dispersal faculties in amphibians have never been critically analyzed.

The dispersal faculties of fresh-water fish also have been underestimated. To begin with, there are many genera and families of so-called fresh-water fish which are, in fact, modified ocean fish and which still have the ability to live in salt water. Such fish are *a priori* disqualified as evidence for or against former land bridges. This leaves the true primary fresh-water fish (Myers, 1938). These are indeed excellent indicators of former continental connections. But there is some evidence that even such species may jump small water gaps under exceptional circumstances (Darlington, 1938). There is well-substantiated evidence for transportation of fish in waterspouts. Furthermore, floods sometimes cover the ocean near the coast with a thin sheet of fresh water and this may serve as a stepping stone between two neighboring islands. If, for example, a single species of Cyprinidae, of the widespread genus *Rasbora*, has succeeded in colonizing Lombok and Sumbawa, this does not necessarily prove the existence of a former land connection between Java-Bali and Lombok. The fact that the other 54 Java species of Cyprinidae were left behind suggests colonization by accident or unusual dispersal faculties for the single species.

It cannot be my task in the present paper to provide a comparative treatment of dispersal faculties in various groups of animals. The time for this has not yet come. But possibly these remarks will stimulate specialists of various groups to correlate the ecological characteristics of each species with its distributional pattern.

The mammalian fauna of the Kei Islands represents a single specific instance only, in which the hypothesis of transoceanic chance dispersal is more successful in explaining the facts than is the assumption of a former land bridge. It seems necessary, in view of the widespread belief in land bridges, to cite additional evidence in favor of transoceanic colonization. Distribution patterns in the Malay Archipelago supply such evidence. There are, for example, four sets of phenomena which have puzzled the land bridge builders and which fit exactly the hypothesis of chance dispersal.

1. Faunal relationships within the Malay Archipelago are independent of the submarine contours (below the 200-meter line) but are closely correlated with the distances of the islands from each other.

It has already been pointed out above that Timor is zoogeographically very close to Wetar, although both islands are separated by an oceanic deep. Equally, the faunal relationship with Sumba is not very great, although both islands are on the same submarine ridge. Good zoogeographic connections also exist between Aru-Kei, between Seran-New Guinea, and between Seran-northern Moluccas, although in all these cases there are no submarine banks that might be interpreted as drowned land bridges. This is supplemented by the surprisingly small zoogeographical relationship of some islands which are situated on the same submarine ridge, such as Sumba-Timor, Alor-Wetar, Timor-Timorlaut-Seran. It can be stated, and there are only few exceptions to this rule, that the fauna of each island of the Indo-Malayan island belt (except on the continental shelves) is the direct product of its accessibility to over-the-water immigrants from other neighboring islands, providing age, size, and ecology are comparable. Islands that are separated by straits of less than 200 meters in depth may have been in continental connection during recent glaciations and as a result may show greater faunal affinity.

2. Slight faunal affinities exist even between geologically unrelated regions.

De Beaufort (1926, pp. 160–161) is rather puzzled about the faunal connections between northern Celebes and Halmahera, between the Philippines and Halmahera, and between the Philippines and New Guinea. The geologist finds no possibility for a land connection between these islands during the late Tertiary or the Pleistocene, which is the period when the faunal exchange must have taken place. It is now obvious that the animals that occur jointly on the island groups mentioned have the ability to cross water gaps of considerable width.

3. The small percentage of endemic species.

If each island or group of islands received its fauna by one or a few land bridges and was then completely isolated, one would expect that most of the species would evolve into endemics during this isolation. It is found, however, that with the exception of a few old islands the number of endemics is rather low. Rensch (1936, pp. 261–262) is perplexed by the fact that so few of the animals of Flores, Wetar, Timor, or other of the eastern Sunda Islands are restricted in their distribution to the Sunda arc. This is true for only 17.5 per cent of the Flores species, for 27 of 297 (=9.1 per cent) of the analyzed Timor species, and for seven of 161 (=4.3 per cent) of the Wetar species. If there had been a continuous land bridge along the inner Banda arc, the percentage should be much higher. What these figures really indicate is that any species that can jump the water gaps of Lombok Strait and of the strait between Alor and Wetar is equally likely to get across to Celebes, to the Moluccas, to Timorlaut, or to Australia. As soon as this happens it will, of course, no longer be restricted to the Sunda arc. The low percentage of species that are widespread on the Sunda arc, but restricted to it, proves the superior dispersal faculty of the species of which the fauna of the Lesser Sunda Islands is composed.

4. The spread of discontinuously distributed mountain animals can be understood only if a great ability to overcome topographical barriers is assumed.

Stresemann (1939, pp. 379–384) points out in his study of the birds of Celebes that many of the species of the mountain forest have an unexpected ability not only to cross stretches of lowland of considerable extent, but even to embark on lengthy transoceanic flights. Such species as *Muscicapula melanoleuca*, *Zosterops montana*, *Dendrobiastes hyperythrus*, *Eumyias panayensis*, *Turdus poliocephalus*, *Phyllergates cucullatus*, *Phylloscopus trivirgatus*, *Bradypterus montis*, *Urosphena subulata*, *Seicercus montis*, and *Dicaeum sanguinolentum* must have made large jumps to get from one mountain top to the next one. Wallace and Rensch have attempted to explain the discontinuous distribution of mountain animals by assuming that the habitats of these species had been continuous during the climatic depression of the Pleistocene. Palaeobotanical and palaeoclimatic research indicates, however, that the drop of the mean temperature in the tropical belt during the glaciation cannot have amounted to more than 1° or 2° C., and this could not have anywhere nearly accomplished a junction of the various mountain forests (Steenis, 1934–1935, pp. 391 ff.). Not even the most liberal construction of land bridges could overcome this difficulty. The same is true of the spread of all animals that are in one way or another narrowly adapted to a discontinuous habitat. Stresemann (*loc. cit.*) calls attention to the fact that there is a considerable variability in the dispersal faculty of mountain birds. Some seem to be poorly endowed with it, and this is particularly true of the mountain species of old islands (like Celebes); others have it highly developed (like most of the above-listed species).

CRITERIA FOR LAND BRIDGES

The above-quoted evidence, in addition to the data accumulated by Gulick (1932), Darlington (1938), and Zimmerman (1942), makes it apparent that a good deal of historical zoogeography will have to be rewritten. Land bridges have been erected in the past with such utter disregard for geological, ecological, and phylogenetic data that almost any land bridge is now under suspicion. The only safe method seems to be to reject any land bridge that does not satisfy a number of basic conditions. The following are some of the criteria which have been developed by recent authors (Stresemann, 1939; Simpson, 1940a; and Mayr, 1941).

1. No species can be quoted as evidence for a former land bridge which occurs also on islands known to be oceanic.

2. All land bridges are temporary, hence all the species that arrived on a certain island by the same land bridge must have the same age. Strikingly different degrees of speciation indicate colonization at different ages, provided all other factors are equivalent. This is well demonstrated by the bird faunas of the Hawaiian Islands, of the Galápagos, of Biak, of New Caledonia, and other islands.

3. A land bridge must have been utilized by a high percentage of the fauna to which it was available. In cases where only a small part of a fauna has used a possible connection, it seems more logical to assume chance dispersal across incomplete barriers rather than to postulate a highly selective land bridge.

4. There are facile transoceanic colonizers in nearly every group of land animals, and others that need true land bridges for dispersal. Each case must be treated on its own merits.

The validity of every land bridge must be tested not only by these four criteria, but it must also be subjected to the additional considerations made by Simpson (1940a).

The evidence on land bridges can be summarized as follows. The majority of the land bridges postulated during the past 50 years are to be rejected for three reasons. First, because they are in conflict with the facts of geology. Second, because they cause more difficulties to the zoogeographer than they explain. The observed distribution patterns are not those that one would expect on the basis of the postulated land bridges. The third reason is that these land bridges are unnecessary, because the existing patterns of distribution can be well explained without them. This is obvious as soon as one realizes the enormous dispersal faculties of most animals as well as the fact that extinction in intermediate areas is the reason for most of the now existing discontinuities.

Results of the New Zoogeographic Method

The decline of the land bridge concept results in a changed attitude towards many zoogeographic problems. This will be illustrated only by a single instance. Ever since Wallace and the Sarasins showed that Macassar Strait indicates a sharp faunal break between Borneo and Celebes and since the geologists found that this faunal break coincides with an ancient geological break, it was taken for granted that all the western elements reached Celebes either via a Java bridge or via a Philippine bridge. It was Stresemann (1939, p. 329) who showed that many of these species, including many flightless ones, could have reached Celebes without a land bridge. As soon as this is admitted, it becomes obvious that Borneo, which is closer to Celebes than either Java or the Philippines, is probably the original home of many of these species. This consideration, incidentally, weakens the Java-Celebes and Philippines-Celebes land bridges, because it drastically reduces the list of the species which "must" have come to Celebes over these two postulated bridges.

Similar considerations can be applied to the colonization of many of the other islands. It results in some instances in the emergence of a completely new distributional picture.

Different Distribution Patterns in each Group of Organisms

It has now become increasingly apparent that the patterns of distribution in island regions depend more on dispersal faculties and ecological requirements of the involved species than on former land connections (particularly where there never have been any). This means that birds, butterflies, and lizards, three groups containing many facile colonizers, will have a different distribution pattern than snakes, mammals or anurans, which are severely handicapped by oceanic gaps, or urodeles and true fresh-water fish, which cross ocean straits only in exceptional cases. Most plants seem to have still greater dispersal faculties than even birds or butterflies. Plants, on the other hand, have much more rigid ecological requirements than most animals. It is for this reason that phytogeographic regions seem to coincide rather closely with climatic regions, while zoogeographic regions, at least in insular districts, tend to be identical with areas of former continental connections, or at least of accessibility.

THE FINDINGS OF THE ZOOGEOGRAPHER

In a way, it has been a great disappointment to the zoogeographer to realize how extensive the dispersal faculties of animals and particularly of flightless animals are. Since it has become obvious that the present distribution of animals is only a poor clue in the analysis of former land connections, it might even be asked whether regional zoogeography can contribute anything at all to facilitate palaeogeographic reconstructions. The answer is, fortunately, yes. There are first the well-balanced continental faunas of islands like Formosa, Borneo, or New Guinea, which prove that these islands have been in recent connection with continents. In all these cases the geological evidence is so strong that it hardly requires confirmation by the biogeographer. Occasionally the zoogeographer can contribute valuable observations to the past history even of well-isolated islands. This is based on the principle of accessibility. Whenever the faunal composition of an island deviates seriously from that which one would expect on the basis of its position in relation to other islands or mainlands, it might give a clue to a change in the geographical configuration. This will be demonstrated with the help of two examples:

1. The Faunal Relationship of Alor to Timor

Alor Island is only 32 kilometers distant from Timor and is thus actually nearer than Wetar (50 kilometers). (See above.) Like Wetar it is separated from Timor by a channel having a depth of more than 3000 meters. The two islands, Alor and Wetar, are of similar size, their geological structure (recent volcanic) seems to be similar, they seem to lie on the same geanticline, and seem to have a very similar climate. Zoogeographically, the two islands are very different as Rensch (1936, p. 162) has shown. Wetar has an impoverished Timor fauna; Alor has an impoverished Flores fauna. The two islands are about 70 kilometers distant, but Kambing Island narrows the distance to 40 kilometers. The greatest depth on the submarine ridge between the islands is about 1260 meters. It is rather mysterious, in view of these facts, why there should be such a striking zoogeographic difference between the two islands. It may be worth while to analyze this contrast a little further.

Among the 78 species of birds which Wetar and Timor have in common, 34 (=43.5 per cent) are not known from the Alor group. On the other hand, such widespread species as *Parus major*, *Acmonorhynchus annae*, *Anthreptes malacensis*, *Lonchura pallida*, *Gracula religiosa*, *Oriolus chinensis*, *Terpsiphone paradisi*, *Hypothymis azurea*, *Dryobates grandis*, *Treron floris*, *Ducula aenea*, *Ptilinopus melanospila*, and *Turnix* (*suscitator*) *powelli* find their eastern limit on Alor and do not expand to Wetar or Timor.

Faunistically there is thus a strong contrast between Alor on one hand and Timor and Wetar on the other. Geographically and geologically Alor and Wetar are in one class and Timor in a different one. This discrepancy is not easily explained. It seems possible, however, that Wetar is a much older island than Alor, even though both are situated on the same geanticline. If this were true, a continuous faunal exchange between closely neighboring Wetar and Timor could have taken place while Flores was rather distant and inaccessible. As Adonara, Lomblen, Pantar, and Alor emerged gradually and successively from the ocean, these islands were populated from Flores, with which island they are in almost complete contact. Thus they acquired an almost pure Flores avifauna. The recent age of Alor is also indicated by the small degree of endemism (only eight slight subspecies among about 75 species of breeding birds). It will be the task of the geologist to prove or disprove this working hypothesis. The only point which I tried to make is that a zoogeographical analysis can yield data of considerable importance to the geologist even if they are not used for the construction of a land bridge.

2. Wegener's Theory and the Position of Australia

All continents and continental islands are, according to Wegener, pieces of a single land mass which broke apart, and the pieces of which eventually drifted into their present position. This is a purely geological theory and it cannot be the task of the zoogeographer to prove or to disprove it. According to

Wegener, Australia, Antarctica, and South America broke off from India-Africa in the early Mesozoic (or late Palaeozoic) and the three continents stayed together until late Tertiary. It is only during the Pleistocene that Australia (including New Guinea) broke off from Antarctica and drifted into the vicinity of the Malay Archipelago. The pros and cons of Wegener's theory of continental drift as applied to the Malay Archipelago have been discussed by Kuenen (1935, pp. 98–109) from the geological point of view and by Rensch (1936, pp. 283–300) from that of the zoogeographer. The foremost geologists of the region (Molengraaff, Umbgrove, Kuenen) have come unanimously to the conclusion "that the Asiatic and the Australian continents at one time [until the late Mesozoic] formed a more or less continuous mass." Kuenen points out that even if continental drift could be proved for other parts of the earth, Australia could not have taken part in this movement, except possibly for a slight counterclockwise rotation around the East Indian Archipelago. Even this event cannot have taken place any later than early Tertiary. The acceptance of such a slight drift would not affect the thesis of the basic stability of the position of the Asiatic and Australian continents to one another. However, according to Wegener, Australia was separated from Asia until Pleistocene by an oceanic gap of 3000 or 4000 kilometers. The zoogeographer is able to test which one of the theories fits the zoogeographic evidence better. According to Wegener, Australia received its fauna from South America (via Antarctica) and established only a very recent contact with the Malay Archipelago and its Asiatic fauna. Accordingly, Australia should be composed of an old Americo-Australian and a very recent Asiatic element. In contradistinction, Australia has always been within reach of transoceanic immigrants from Asia, according to the orthodox geological theory, although this colonization became slowly but steadily accelerated during the period when one after the other of the islands of the Malay Archipelago emerged from the sea. This faunal exchange reached a climax during the Pleistocene glaciations when the continental shelves were largely dry land. The zoogeographic data are in complete agreement with this second alternative and are thus the exact opposite of what one would expect on the basis of Wegener's hypothesis.

The test must be made with groups of animals which have a fair ability of crossing oceanic gaps. Mammals are, therefore, ruled out. As Simpson (1940b) has shown, there is good reason to believe that the ancestors of both the Australo-Papuan marsupials and of the rodents have reached their present home by rafting. This involves only two or possibly three separate colonizations, which is too small a number to test the above-made hypothesis. Birds, on the other hand, are well suited for this purpose. If there had been throughout the Tertiary a continuous series of colonizations of Australia from Asia, one would expect that the earliest colonizers had changed to separate familes or subfamilies, later ones to separate genera, still later ones to separate species, and the most recent arrivals to separate subspecies. This is exactly what we find when we examine the bird fauna of Australia. First there are some old endemic families and subfamilies, of which the nearest relatives are uncertain. This includes the Dromaiidae, Casuariidae, Megapodiidae, Loriinae, Cacatuinae, Platycercinae, Podargidae, Menuridae, Atrichornithidae, Grallinidae, Artamidae, Neosittidae, Meliphagidae, Struthideinae, Ptilonorhynchidae, and Cracticidae. Important is the point that not a single one of these families is more closely related to a South American family than to an Old World family. There is thus no evidence among the old Australian bird element for a former connection with South America.

The next oldest element is composed of a number of families and subfamilies which probably reached Australo-Papua during early or middle Tertiary and which are plainly related to Old World families. This includes the Pedionomidae, Ptilinopinae, Pachycephalinae, Sphecotheridae, Cinclosomatinae, Acanthizinae, Pardalotinae, and Paradisaeidae.

The third group consists of the genera which are endemic in Australo-Papua, but which are clearly related to Asiatic genera. This group may include some Miocene arrivals but is probably composed mainly of Pliocene colonists. It would lead too far

to give the full list and I shall content myself in listing only a selection: *Synoicus*, *Geopelia*, *Irediparra*, *Notophoyx*, *Dupetor*, *Erythrotriorchis*, *Uroaetus*, *Lophoictinia*, *Ieracidea*, *Syma*, *Dacelo*, *Tanysiptera*, *Cacomantis*, *Misocalius*, *Chalcites*, *Eudynamis*, *Rhipidura*, *Myiagra*, *Machaerirhynchus*, *Seisura*, *Arses*, *Monarcha*, *Microeca*, the *Poecilodryas* group, *Pteropodocys*, *Climacteris*, *Zonaeginthus*, *Erythrura*, *Aplonis*, *Corcorax*, and others.

Even more recent are those colonists which diverged only specifically, since they arrived in Australo-Papua late in the Pliocene or early in Pleistocene. The exact time of arrival is, of course, uncertain in view of the absence of fossils and with the probability of different speed of evolution in different lineages. This list includes the following species:

Coturnix pectoralis
Turnix (6 species)
Columba norfolkiensis
Rallus pectoralis
Rallus philippensis
Porzana fluminea
Podiceps novaehollandiae
Podiceps poliocephalus
Eupodotis australis
Grus rubicunda
Platalea flavipes
Nycticorax caledonicus
Botaurus poiciloptilus
Circus assimilis
Circus approximans
Accipiter novaehollandiae
Accipiter fasciatus
Accipiter cirrhocephalus
Hieraaëtus morphnoides
Elanus axillaris
Elanus scriptus
Aviceda subcristata
Falco longipennis
Falco hypoleucus
Falco cenchroides
Tyto novaehollandiae
Tyto tenebricosa
Ceyx azurea
Ceyx pusilla
Halcyon (4 species)
Merops ornatus
Eurostopodus (2 species)
Collocalia spodiopygia
Collocalia vanikorensis
Cuculus pallidus
Centropus phasianinus
Hirundo tahitica
Hirundo nigricans
Hirundo ariel
Coracina papuensis
Coracina robusta
Coracina lineata
Edolisoma tenuirostre
Megalurus gramineus
Megalurus timoriensis
Zosterops lateralis
Zosterops lutea
Lonchura castaneothorax
Lonchura flaviprymna
Oriolus sagittatus
Oriolus flavocinctus
Corvus coronoides
Corvus bennetti

Finally there is a group of about 40 species which reached Australia so recently that only subspecific differentiation has occurred.

The zoogeographic data are thus in striking accord with the assumption of orthodox geology that the relative position of Asia and Australia has not changed materially since the Mesozoic, and that tectonic processes have been responsible first, for the isolation of the two continents by sea, and second, for the establishment of a connecting island belt. The accessibility of Australo-Papua to Tertiary colonizers from Asia becomes even more apparent if we compare the fauna and flora of New Guinea rather than of Australia with that of Malaysia.

There are additional objections to the application of Wegener's drift theory to the Australo-Papuan region. The Solomon Islands and the Bismarck Archipelago, for example, are, according to Wegener, parts of the Moluccas-Sunda Islands chain which split off when the Australo-Papuan block "crashed" into this chain of islands. According to Wegener, the fauna of the islands east and west of New Guinea should have a Malayan character as against an "Australian" fauna on New Guinea. Actually the fauna of the Solomon Islands and of New Britain is strictly an impoverished Papuan fauna, except for a few endemics of uncertain relationship. This constitutes another objection to Wegener's hypothesis.

The main theme of the present discussion is not to disprove Wegener's theory. Rather it is to show that zoogeography is a very useful and illuminating science, even if stripped of all its land bridge building tendencies. Zoogeographic data can be applied to the solution

of many palaeogeographic problems. In fact, an unsuspected wealth of material is available to the comparative biogeographer. The investigation presented above gives some hints on certain lines of approach which might yield valuable results to other students. The distribution of mammals, reptiles, amphibians, and invertebrates will have to be subjected to an analysis similar to that which I have applied to birds before we can hope for a balanced picture of the history of colonization of the Malay Archipelago.

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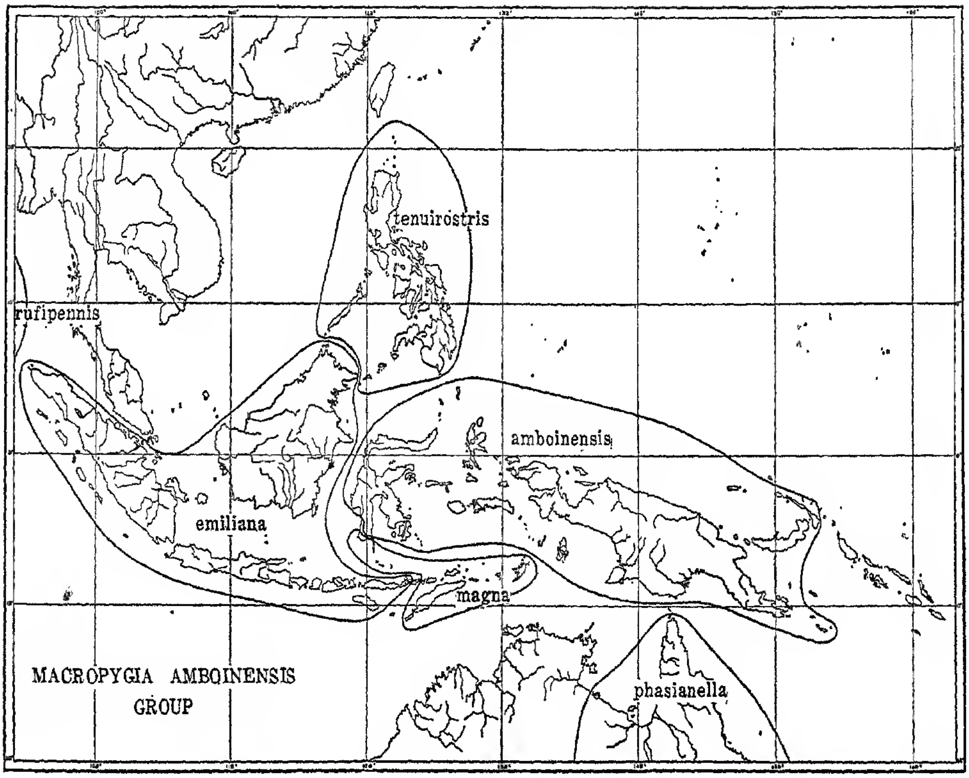

FIG. 1. The distribution of the *Macropygia amboinensis* group. The six subgroups represent each other geographically. There is no overlap even in south Celebes, where *magna* is restricted to the more or less arid lowlands, while *amboinensis* is found in the more humid hill country.

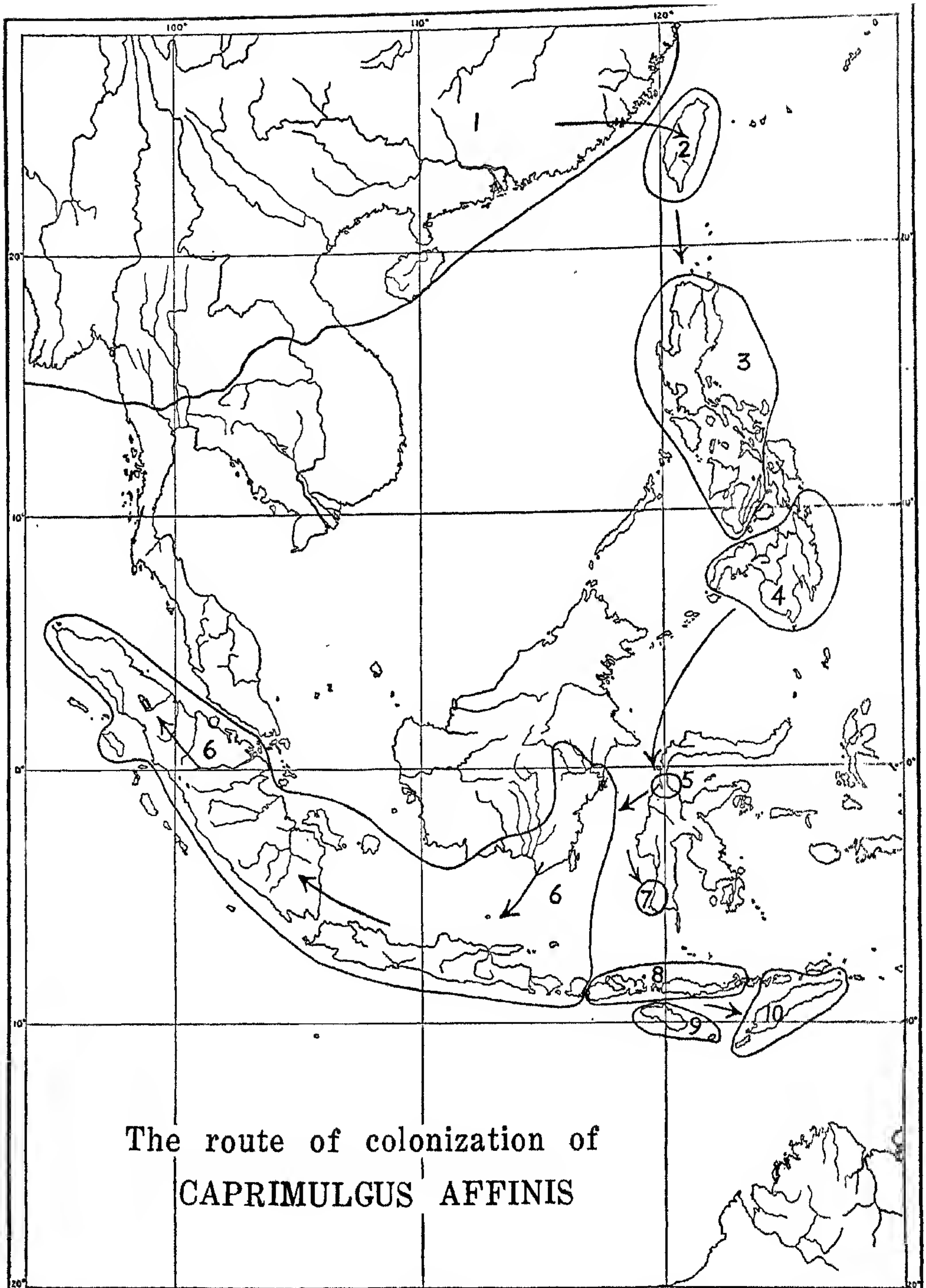

FIG. 2. *Caprimulgus affinis* entered the Malay Archipelago via Philippines and Celebes. It has not succeeded in reaching Australia across Timor Strait, like *Cisticola exilis* or many other grassland species with a similar distribution pattern. 1, Continental races of the *monticolus* group; 2, *stictomus;* 3, *griseatus;* 4, *mindanensis;* 5, *propinquus;* 6, *affinis;* 7, subspecies, near *affinis;* 8, *undulatus;* 9, *kasuidori;* 10, *timor-*

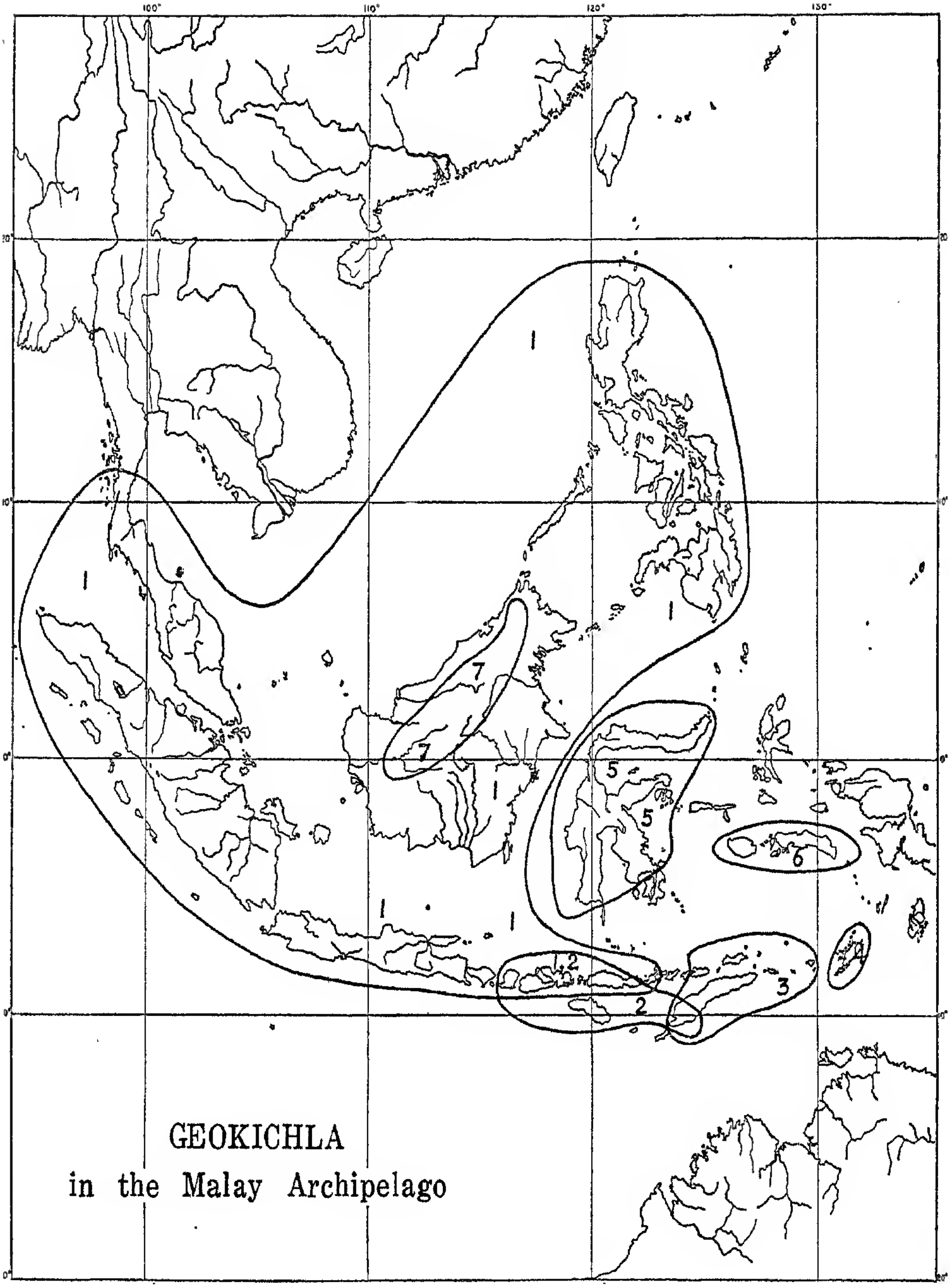

FIG. 3. The *Geokichla* species in the Malay Archipelago. 1, *Interpres;* 2, *dohertyi;* 3, *peronii;* 4, *schistacea;* 5, *erythronota;* 6, *dumasi-joiceyi;* 7, *everetti.* The first six of these are closely related and are still largely geographical representatives. Overlaps occur between *interpres* and *dohertyi* on Lombok, Sumbawa, and Flores, and between *dohertyi* and *peronii* on Timor.

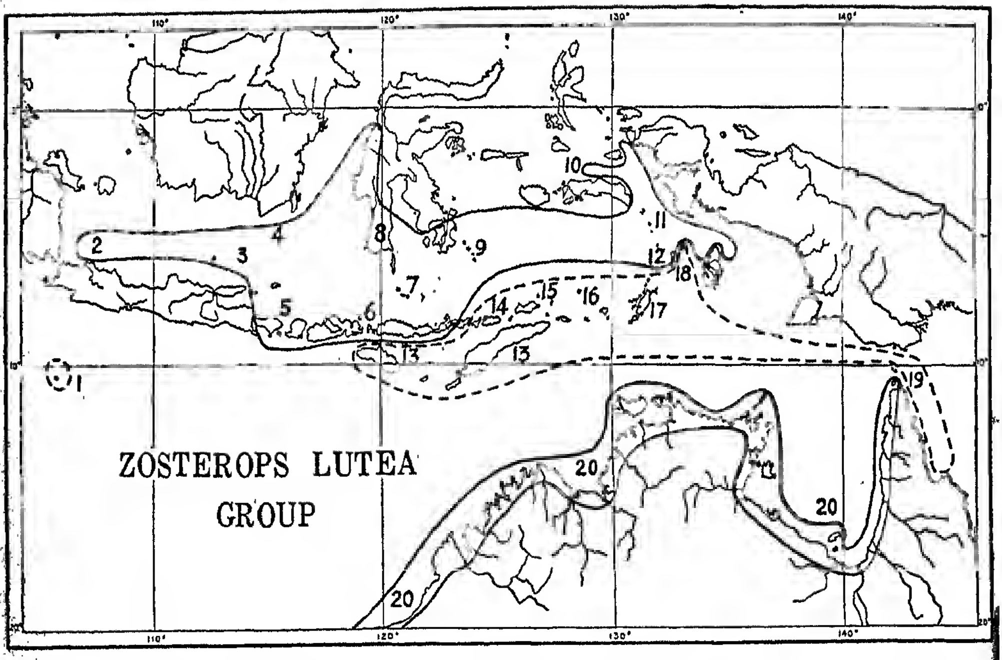

FIG. 4. The distribution of the *Zosterops lutea* group. 1, The white-bellied *natalis*. 2–12, The yellow *chloris* subgroup: 2, *maxi;* 3, *solombensis;* 4, *zachlora;* 5, *periplecta;* 6, *sumbawensis;* 7, *kalaotuae;* 8, *intermedia;* 9, *flavissima;* 10, *tudjuensis;* 11, *chloris;* 12, *uropygialis*. 13–19, The white-bellied *citrinella* subgroup: 13, *citrinella;* 14, *harterti;* 15, *lettiensis;* 16, *bassetti;* 17, *griseiventris;* 18, *grayi;* 19, *albiventris*. 20, The yellow-bellied *lutea* subgroup. Closely related species to the east are *griseotincta*, *rennelliana*, and the *rendovae* subgroup.

BULLETIN No. 1

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BENARES

CONTENTS

The Age, Origin and Classification of the Rivers of India

BY

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The Age, Origin and Classification of the Rivers of India*

BY

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In India rivers perform a very important role in her national economy. Connected with the varied relief and geomorphology of the country there are various types of rivers in India. The authors of "A Sketch of the Geography and Geology of the Himalaya Mountains and Tibet", Part III, pp. 176-178 proposed a regional classification of the Himalayan rivers and fixed the Tista, the Kali, and the Sutlej as the dividing lines. But such a classification may group rivers entirely of different origin and ages. For instance, in the Assam Himalayas the Brahmaputra and the Tista are grouped together, but the two rivers are entirely of different ages and have entirely different histories. The same is true of the Indus and its tributaries, the Beas, Ravi, Chenab, and the Jhelum.

The Himalayan Rivers

The present author has proposed the following classification of the Himalayan rivers :—

(1) The Tibetan or the Pre-Himalayan rivers.

(2) The Great Himalayan rivers. They may be post-Mid-Miocene in age when the Himalayas had undergone its second phase of upheaval.

(3) The Lesser Himalayan rivers.

(4) The Siwalik Rivers. These are definitely of post-Pliocene age.

The Tibetan Rivers :— The three rivers, viz., the Indus, the Sutlej, and the Brahmaputra form a type by themselves. They

*Inaugural Address by the President, delivered before the Society on the 27th August, 1946.

take their rise in Tibet, a considerable distance north of the Great Himalayas marking the line of the highest peaks. They undoubtedly represent the oldest of the Himalayan rivers. It is familiar that these rivers are older than the mountains through which they flow. The upheaval of the mountain and the erosion by the rivers went on *pari passu*, so that they kept their channels open. They represent, of course, the well-known antecedent type of drainage. For a considerable distance they flow in a longitudinal direction and then they suddenly break across the Himalayas where they have cut very deep transverse gorges. The Indus and the Sutlej first flow to the north-west and after cutting through the Himalayas follow a south-west trend. These three rivers have their sources located close together, but the Brahmaputra flows to the east. These rivers are definitely Tibetan and the name of the Brahmaputra in its upper reaches is Tsangpo.

The Great Himalayan Rivers:— The second group of rivers comprises the Ganges and its following tributaries, the Jumna; the Sarda, the Gogra, the Gandak and the Kosi. It may be noted that the Tista and the Manaas, the two tributaries of the Brahmaputra, also belong to this group. These rivers have their sources in the glaciers generally descending from the Great Himalayas and are evidently younger than the three antecedent rivers, referred to above. The Bhagirathi rises from the Gangotri glacier behind the Kedarnath peaks, which has its source known as *Gau Mukh* at an altitude of 13,000 feet above the sea level. The source of the Jumna lies in the Tehri State, about five miles north of the Jamnotri hot springs. Next the headwaters of the Sarda or Kali or the Chauka river lie in the north-eastern part of Kumaun.

The Gogra:— It may be noted that the Gogra, which is known as the Karnali in its upper course, drains the Trans Himalayan trough, 200 miles in length from Gurla Mandhata almost up to the Diji Pass. It has two arms: a north-eastern and a north-western. The latter is about a 100 miles in length, while the north-eastern arm, newly discovered, is even longer.

The Gandak:— The two tributaries of the Gandak, viz., the Kali Gandak and the Trisuli Gandak have carved out gorges

through the Great Himalayan range and now drain the trough between that range and the Ladakh range of Tibet. The two other tributaries, viz., the Burhi Gandak and the Marsyandi have cut back behind the Great Himalayan crest but have not reached the trough behind.

The Kosi :— It is also known as the Sapt-Kosi, i.e., formed by the union of seven rivers. The six great branches from west to east are the Indrawati, the Bhote Kosi, the Tamba Kosi, the Dudh Kosi, the Arun and the Tamur Kosi. The three branches, the Indrawati, the Dudh Kosi, and the Tamur Kosi take their rise from the Himalayan glaciers. The Dudh Kosi drains the southern slopes of Mount Everest, while the Tamur Kosi drains the western slopes of Kanchenjunga. The Arun is the biggest branch which has cut a gorge backwards through the Great Himalayan range and now drains the trough in the rear.

The Tista :— This river takes its source from the glaciers of the Great Himalayan range, particularly those descending from Kanchenjunga, but like some other rivers it has cut through the crest line by head erosion.

Headward Erosion :— It is noteworthy that many of the Himalayan rivers have cut backwards by head erosion behind the Great Himalayan crest and in some cases have even reached the trough in the rear. Conspicuous examples of this may be cited such as some of the branches of the Ganges, the Karnali or the Gogra, and the Arun which represents the largest branch of the Kosi. This is believed to be due to the fact that there is greater rainfall on the southern than on the northern slopes of the Himalayas.

The Lesser Himalayan Rivers :— The third group comprises those rivers which take their rise in the Lesser Himalaya or between the Lesser Himalaya and the Great Himalaya. These rivers comprise the four affluents of the Indus, viz., the Beas, Ravi, Chenab and the Jhelum. Proceeding eastwards the Khoh, the Ramganga, the Rapti and the Bhagmati also belong to this group.

Commencing with the Punjab rivers, the Beas rises in the Pir Panjal range at the Rotang Pass at an altitude of 13,000 feet above the sea level. The next river Ravi has its source in a mountain knot formed by the joining of the Lesser Himalayan ranges. It rises in the basin of the Bangahal and drains the southern slopes of the Pir Panjal and the northern slopes of the Dhaula Dhar. The Chandra and the Bhaga take their rise on the opposite sides of the Bara Lacha Pass (16,047), the Chandra descending on the south-east, while the Bhaga doing from the north-west. They unite at Tandi to form the Chenab river. The Jhelum is a river of Kashmir. One of its important sources is in the lake of Shesha Nag at the head of its Lidar tributary. Proceeding eastwards comes the Ramganga West which belongs to this group. It has its source in the Garhwal district, some distance to the south of the main range of the Himalayas. The Rapti has its source in the lower ranges of Nepal. The Bhagmati takes its rise near Katmandu in Nepal and flows through a small valley behind the Mahabharat range which occupies an analogous position between the great snowy range and the Siwaliks as the Mussourie range does in Garhwal.

The Siwalik Rivers :— Some rivers take their rise in the Siwalik hills. Several instances could be adduced of such rivers but the Hindan and the Solani are quite representative, which take their rise from the Siwaliks near Dehra Dun. These rivers are definitely post-Pliocene in age.

A brief account of the Hindan is given here. It is a river of the United Provinces, rising on the southern slopes of the Siwaliks in the Saharanpur district. It flows generally towards the south-west. After draining the central portions of the Saharanpur, Muzaffarnagar, and Meerut districts it meets the Jumna in the district of Bulandshahar after a career of 160 miles. It may be noted that a part of its channel forms an important link between the Ganges and the Jumna. From the Upper Ganges Canal, water can be passed into the Hindan and then by means of a cut made in 1877 into the Jumna above Okhla. The scheme is intended to increase the water supply of the Jumna for the Agra Canal.

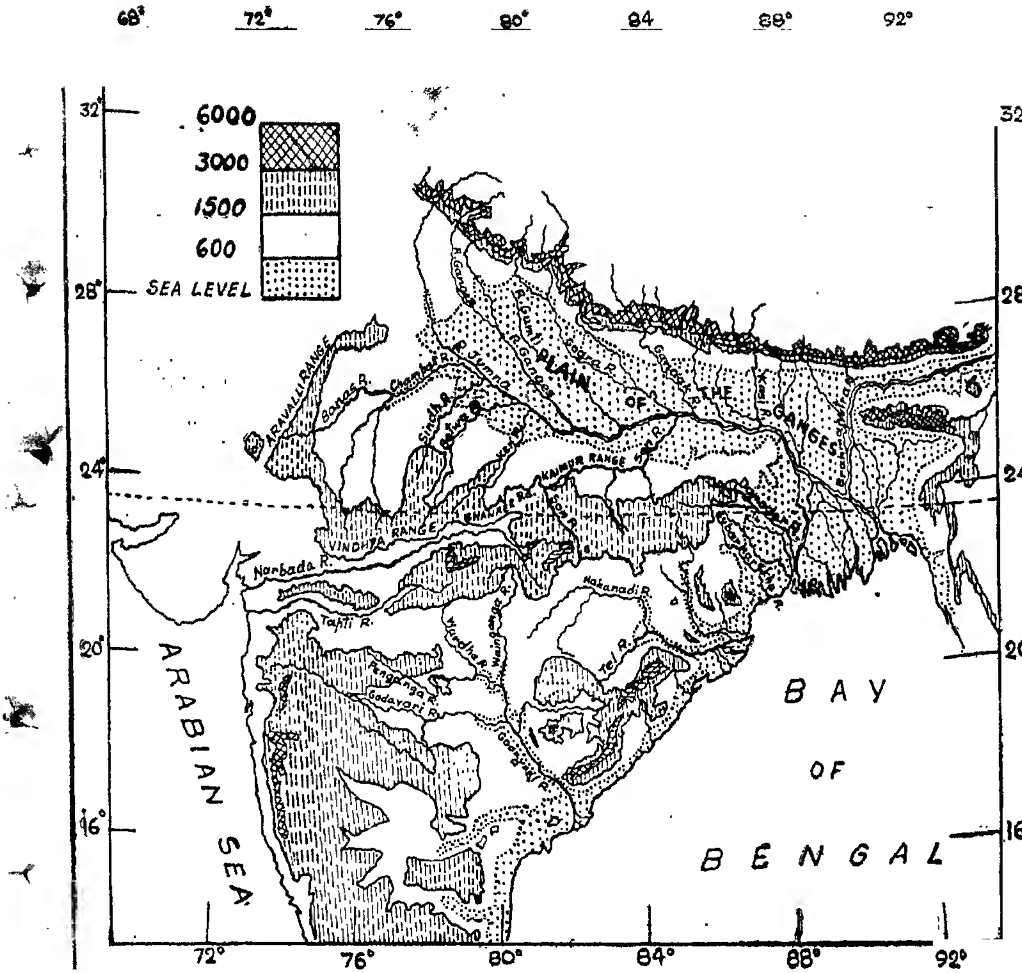

Fig. 1— Note the courses of the Chambal, Sindh, Betwa, Ken, Son, Damodar, Subarnarekha, Mahanadi, Wainganga, Wardha, Narbada, and Tapti. It will be observed that these rivers rising from the highlands of Central India definitely represent a radial type of drainage.

Post-Pleistocene Rivers

These rivers take their rise in the Indo-Gangetic plains. The Older Alluvium has been proved to be of Pleistocene age and these rivers cutting it, must be of subsequent age. It would be perhaps surprising to find that an important river like the Gumti has it source in the plains west of Kalinagar and Madho Tanda in the Pilibhit district. Lucknow is situated 180 miles from its source. Below Lucknow, the river winds considerably through the Bara Banki, Sultanpur and Jaunpur districts. Between Lucknow and Jaunpur it covers twice the distance as compared to that in a direct line. It joins the Ganges near Saidpur in the Ghazipur district, after a total course of nearly 500 miles.

Instances of such rivers could be multiplied but to the residents of the United Provinces and particularly those of Benares, the example of the Barna may be cited. It rises in the plains on the borders of the Mirzapur and the Allahabad districts. It is joined by the Bishui and the combined waters form a fair-sized river which follows a very meandering course. After flowing through the Civil Station of Benares it bends to the south-east and joins the Ganges below the railway bridge. The confluence is considered a sacred spot and is the scene of many bathing festivals. Throughout its course, the river has high banks. The floods of the year 1943, which damaged the bridge at Benares to such an extent that a new one had to be erected, were unprecedented practically for the last 80 years. Relief work had to be organised in the affected areas.

Radial Drainage

The next type of drainage is that which is connected with the highlands of Central India. It must be stated that this system is not properly understood. From these highlands rivers flow out practically in all directions and thus definitely represent a radial type of drainage. The rivers flowing to the north comprise the Chambal and its tributaries Banaas, etc, the Sindh, Betwa and the Ken. These flow northwards and are tributaries of the Jumna. The next important river rising from these highlands is the Son, which meets the Ganges near Dinapur.

Proceeding eastward is the Damodar river which practically has an easterly course and joins the Ganges in its deltaic portion.

The Subarnarekha is the next river which has its source in these highlands and after following a south-easterly course flows into the Bay of Bengal, some distance west of the mouth of the Hooghly. The Mahanadi and its tributaries, which take their rise in these highlands, follow a somewhat easterly course.

So far we have considered rivers flowing to the north and the east. Now we deal with the rivers which rise from these highlands and flow to the south. The most important of these comprise the Wainganga and the Wardha which become tributaries of the Godavari.

Now we have the rivers which follow a westerly course and to this category belong the important Narbada and the Tapti. It is generally presumed that the Narbada and the Tapti show an exceptional behaviour in flowing to the west. But it is not realised that these rivers form part of the radial drainage of the highlands of Central India. Above have been enumerated the rivers which definitely take their rise in these highlands and flow in all directions, north, east, south and west (See Fig. 1) .

It is practically with the source of the Godavari about 20° N. latitude that the main Peninsular rivers follow an exclusive easterly course. A little north of this line are the rivers, noted above, which descend from those highlands and follow a radial course.

But it may be noted here that the upwellings of the Deccan Trap introduced complications in the geomorphology of Peninsular India. These outpourings of the lava obliterated the previous ancient floor and a new drainage on this new topography had to be established. But it must be emphasized here that the flows of the Deccan Trap naturally followed the previous slopes of the country. Thus although a new formation was introduced yet the general slopes remained unaffected as the liquid lava like water would not flow against gravity. The Deccan Trap introduces, therefore, another factor in the classification of these rivers which can be grouped as follows:– the Chambal,

the Sindh, the Betwa, the Narbada and the Tapti. These are of younger age and have their origin located in the Deccan Trap, while the remaining have their sources in the older rocks. Furthermore, it is noteworthy that the tributaries, the Chambal, the Sindh, the Betwa and the Ken are older than the main river of today, i. e., the Jumna. Likewise, the Son is older than the Ganges in which it discharges its waters.

Easterly Drainage

Next we consider the easterly drainage of the Peninsula. It comprises the Godavari, the Kistna, the North Pennar the South Pennar and the Cauvery. These rivers have again to be classified into two groups: (i) the rivers of the Deccan Trap and (ii) the rivers of the older rocks. Thus the Godavari, the Bhima and the Kistna, which rise in the Deccan Trap, are definitely younger than the Cauvery, the North and the South Pennar and the Tungabhadra, rising in the older rocks.

Two theories have been advanced to explain the easterly drainage of the Peninsula. First, the Deccan plateau received an easterly tilt at the time of the upheaval of the Himalayas. It is not clear, however, how the thrusts coming from the north could give an easterly tilt to the Deccan plateau. Secondly, it represents the eastern half of the drainage, while the western half was submerged towards the close of the Mesozoic era. The author is inclined to the latter view as it is also in agreement with the disruption of the Gondwanaland.

It is also commonly alleged that the Peninsular rivers have reached their base level of erosion. To get a true idea one should visit the Narbada near Tilwara Ghat and follow the course downstream for some miles. Nothing can be far from the fact of the river having reached its base level of erosion. The bed of the river is very uneven indeed. In places, the bed is traversed by ridges of rocks across its channel, while in others the rocks are seen projecting above water and finally there are falls and cascades. The famous Dhuan Dhar falls and the gorge of the Narbada near Bhera Ghat are cut in the Marble Rocks comprising the dolomitic marble of Dharwar age. Such falls occur in some

of the other peninsular rivers also. It has been shown above that all rivers of the Deccan are not of the same age and in fact the rivers of the Deccan Trap are only a little older than the Himalayan rivers. It would, therefore, not be correct to generalise for the whole of Peninsular India. When referring to a river of Peninsular India, either the river or at the most the contemporaneous group must be specified.

Westerly Drainage

These comprise the short and torrential rivers which take their rise in the Western Ghats and discharge their waters into the Arabian Sea. The Narbada and the Tapti discharge their waters into the Gulf of Cambay. Immediately south of the mouth of the Tapti and almost contiguous with it is the mouth of the Mundhola river. Farther south are the Ambika, Damanganga, Vaitarna and the Ulhas rivers. The latter, in its lower course, forms the well-known Bassein creek on which Bassein is situated. South of the island of Bombay are the Amba, Kundalika, Savitri, Vashishti, Shastri, Kajvi and the Vaghotan rivers. These rivers are enumerated in order from north to south and as far as 16° 30′ North latitude. It is noteworthy that all these rivers have their courses in the Deccan Trap. It may be noted that the scarp edge of the Western Ghats facing the Arabian Sea and forming the watershed as far as the Decean Trap flows extend, is quite precipitous and well-marked. The last river of this group is the Gad which rises in the Deccan Trap but has its lower course in the gneisses.

Farther south are the Tilari, Candoapai, Rachol, Kalinadi, Gangavalli, Sharavati, Haladi, Sitanadi and the Swarnanadi. Lower down in South Canara are the Gurpur and the Netravati rivers. These rivers have their mouths located near Mangalore. They take their rise in the gneissic country but their lower course is in Recent deposits. Below Mangalore is the Payaswani river which also flows on the gneissic crystalline rocks. The important rivers draining Malabar are Valapattanam, Beypore and the Ponnani. The important rivers of Cochin and Travancore are the Alwaye, Chalkudi, Periyar, Pambiyar and

Tambraparni. These rivers again are of the same age as the rivers of Malabar, noted above.

About the Periyar it is familiar that it represents the river which nature intended to flow into the Arabian Sea but by human ingenuity it has been made to flow into the Bay of Bengal. A dam was built across a gorge in Travancore State, 3,000 feet above sea level. The waters of the lake are taken to the Madura plains through a tunnel 5,700 feet in length and irrigate 133,000 acres in a precarious tract of the Madura district.

Thus it will be observed that these rivers are of two widely different ages :— (i) the first group is of post-Archaean (the term is used in a generic sense) age and it comprises the rivers flowing in the extreme south and as far as the Gad river in the north the nature of whose course has been referred to above. (ii) The second group includes the rivers commencing with the Vaghotan river in the south to the Tapti and the Narbada in the extreme north. All these rivers are definitely of post-Deccan Trap age.

It is further noteworthy that these rivers, being short and torrential and affected by the Arabian Sea Branch of the monsoons, and gales, do not build any deltas but wide estuaries at their mouths.

The West Coast of India owes its origin to the breaking up and foundering of the part of Gondwanaland under the Arabian Sea but there is no doubt that the coast underwent further submergence later as is proved by a number of facts. The submerged forests of Bombay offer a clear testimony to that effect. The nature of the creeks with branching inlets and the characteristic backwaters or *kayals* lend further support to this conclusion.

Finally, it may be noted that these short rivers possess great potentialities. These torrential rivers have no doubt many falls and cascades in their courses and especially during the monsoons they have abundant water, which, if impounded as in the case of the Periyar project, can be very beneficial for hydro-electric and irrigation purposes. With careful investigation and planning, the author is of opinion that several projects like the Periyar could be developed.

BULLETIN No. 7

OF

National Geographical Society of India,

BENARES

CONTENTS

Torrential Fishes and the Significance of their Distribution in Zoo-Geographical Studies

BY

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Torrential Fishes and the Significance of their Distribution in Zoo-Geographical Studies.[1]

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Director, Zoological Survey of India, Benares.

Dr. Radhakrishnan, Professor Chhibber, Ladies and Gentlemen

When Professor Chhibber invited me to speak to you this afternoon, I did not know that I was being called upon to address the first Anniversary Meeting of the National Geographical Society of India and neither was I aware that our eminent and distinguished countryman, Dr. Sarvapalli Radhakrishnan, had consented to honour the meeting by presiding over it. Though I feel somewhat embarrassed by the grandeur of the occasion, all the same I greatly appreciate the honour you have done to me by asking me to address the meeting. Your choice of a Non-geographer as speaker augurs well for your Society, for you have shown a breadth of vision and vast scope of your investigations in asking a zoologist to deliver a lecture at the Anniversary Meeting. Geography, as you know, is an important border line science, which needs the help and co-operation of several other branches of basic science. It may here be recalled that the illustrious founder of the Zoological Survey of India, the late Dr. Nelson Annandale, laid down as one of the main duties of the Department "to obtain the fullest possible information about the systematic and geographical Zoology of the Indian Empire." The distribution in space of many of the species and genera of the animal kingdom provides evidence of the geographical changes that have taken place and of the evolution in past ages of the various land-masses around India that have combined to produce the character of the continent of Asia as we know it today. All the officers of the Zoological Survey of India, after

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[1] The First Anniversary Address delivered before the Society on the 13th September, 1947.

familiarising themselves with the systematics of the group of animals, in the study of which they may be interested, are drawn into zoo-geographical problems, for the study of taxonomy and distribution of animals is still of fundamental importance in its application even to such utilitarian sciences as Agriculture, Animal Husbandry, Fisheries, Forestry, Medicine and Public Health.

Since 1919, I[1] have been interested in the study of modifications and structural adaptations undergone by the torrential fauna, particularly fishes, and of late my investigations into the systematics of the hill-stream fishes and their distribution have led me to certain remarkable conclusions regarding the palaeogeography of India[2]. It is my intention to deal this evening with only one aspect of these studies, the Satpura-Vindhyan Trend of mountains, for it will be easy for the Benares students to investigate further the geographical problems I shall lay before you by paying visits to the spurs of the Vindhya Mountains in the Mirzapur District only a few miles away from here.

My subject for this evening's lecture resolves itself into four topics, namely, (i) torrents, (ii) fishes inhabiting torrential streams, (iii) distribution of torrential fishes and (iv) palaeogeographical significance of this distribution. Though one subject leads to the other imperceptibly, I shall deal with each separately so that the main conclusions are easily grasped by all.

Ecological Aspect of Torrential Streams

In areas, where the rainfall is heavy and the drainage is good, the streams swell up greatly and often suddenly after a heavy downpour and acquire the characteristic impetuousity of a mountain torrent. The streams in the neighbourhood of Cherrapunji, a place known all over the world for its heavy rainfall, about 458 inches *per annum*, may be taken as an example. Mr.

[1] Hora, S. L., *Phil. Trans. Royal Soc. London*, 218, pp. 171-282 (1930)
[2] Hora, S. L., *Proc. Nat. Inst. Sci. India*, X, pp. 423-439 (1944).

PLATE I

Bird's-eye view of the Nong-priang stream from the Cherrapunji plateau.

Oldham, the famous geologist, "took an opportunity of visiting one of the streams in these hills after a heavy and sudden fall of rain. The water had then risen only about thirteen feet above the level at which it stood a few days previously; the rush was tremendous—huge blocks of rock measuring some feet across, were rolled along with an awful crashing almost as easily as pebbles in an ordinary stream. In one night a block of granite, which I calculated to weigh upwards of 350 tons, was moved for more than 100 yards, while the torrent was actually turbid with pebbles of some inches in size, suspended almost like mud in the rushing stream."[1] By their own action, such streams carve out for themselves deep and narrow gorges. For example, the Nong-priang stream below the Cherra Plateau flows some 3,000 feet below the level of Cherrapunji but is visible in the valley as a silvery streak from above (See Plate 1). Other streams in this region have the same characteristics. The stream beds are usually formed of big boulders and stones interspersed with rapids and waterfalls. Certain types of fish, such as Trout and Mahseer, can negotiate rapids and low falls (See Plate II, Fig. 1) through sheer muscular effort, but when a fall is more than 15 to 20 feet-high, such as the sacred 90 feet Kapil Dhara Fall of the Narbada River a short distance below Amarkantak (See Plate II, Fig. 2), it forms a barrier for the migration of fishes. Sometimes behind such high falls, there are wet rocks kept moist either by the spray of water from the fall or by a small trickle of water from the rocks above. Certain types of fish provided with special organs of adhesion can crawl up such wet surfaces but there is generally a limit to their migration as they cannot stay out of water for long. Besides the exceptions referred to above regarding the leaping or crawling up the waterfalls, the torrential fishes live on, under or among the rocks and boulders over which water flows very swiftly. If we analyse this habitat, we shall notice that the fishes which live under rocks and stones among pebbles and shingle have to contend with less force of rushing water, while those that live on the rocks have to bear the

[1] Oldham, R. D., *Mem. Geol. Surv. Ind.* I, p. 174 (1850).

greatest ferocity of the current. Accordingly, small loaches (*Nemachilus*) or loach-like fishes (*Amblyceps*, *Olyra*, etc.) are met with at the bottom and limpet-like (*Balitora*, *Glyptosternum*, etc.) or specially modified fishes (*Garra*, *Glyptothorax*, *Pseudecheneis*, etc.) are found on rocks.

Main Ecological Characteristics of Torrential Fishes

Now for a few minutes, let us consider the main environmental factors which have induced remarkable structural adaptations in torrential fishes. We have already referred to the swiftness of the current and the various forms of the organs of attachment. There is apparently little food in the bare hill-streams but the fishes living on rocks have acquired the habit of rasping off algal slime or encrusted organisms from rocks and stones. I need not detail here on the modifications undergone by the mouth parts of these fishes, but suffice it to say that they have become incapable of feeding in deep water or on a muddy bottom. Another factor of importance is the highly oxygenated nature of the water of torrential streams which has induced remarkable structural modifications in the organs of respiration. Owing to richness of water as regards its oxygen contents, the gill-openings become restricted and the gills themselves are also reduced, with the result that such fishes cannot live for long in sluggish waters generally poor in oxygen. It will thus be seen that for their migration from one place to another, even a deep river, a sluggish stream or a marsh can act as a barrier. Sometimes they may be washed down into rivers but they are likely to perish ultimately unless they happen to be carried into hill-streams again. Their dispersal can only be through the continuity of torrential streams.

Fishes of the Family Homalopteridae.

I have referred above to a variety of hill-stream fishes and many more could be mentioned but I shall particularly deal this evening with the Homalopteridae, a remarkable family of

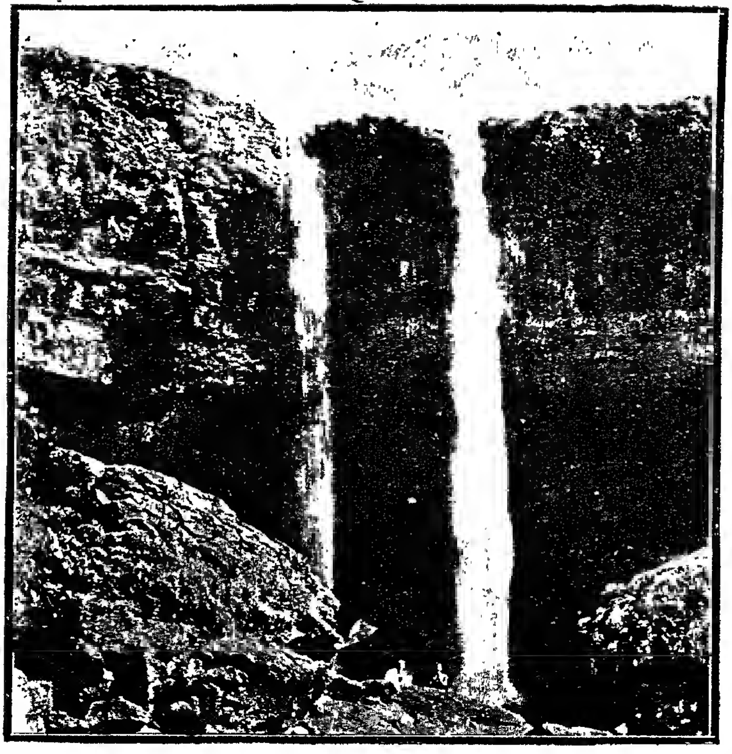

Fig. 1—The sacred fall of Kapildhara, the Narbada River, about 8 miles from Amarkantak. It is about 90 feet in height and acts as an effective barrier for the movements of fishes.

Fig. 2—A series of small falls with pools at their bases in a stream near the Tista Bridge, Eastern Himalayas. Fishes can negotiate such obstructions in their movements.

torrential fishes found throughout south-eastern Asia. I[1] have advanced the view that it is a polyphyletic family, Gastromyzoninae having been derived from the Cobitidae (Loaches) and Homalopterinae from the Cyprinidae (Carps). Owing to parallelism in the evolution of the two stocks they look superficially alike. They adhere to rocks like limpet and in some of them the entire ventral urface inclusive of the paired fins forms one large sucker. The *Gastromyzon* of Borneo is one such fish. The gill-openings are reduced to small apertures dorso-laterally. There are, however, stages in the evolution of such an extreme form as *Gastromyzon*, both among the Gastromyzoninae and the Homalopterinae. Most of the remarkable structural peculiarities so characteristic of the Homalopteridae can be traced back to three principal factors in their environment current, high percentage of oxygen in torrential waters and the nature of the food available in the hill-streams.

Distribution of the Homalopteridae in India

I have indicated above that the Homalopterid fishes are found in torrential streams throughout south-eastern Asia, Southern China, Cochin-China, Siam, (Thailand), Malay Peninsula, Burma and India. I shall not have time to deal with its entire range of distribution this evening but in India proper, the Homalopteridae have a discontinuous distribution. *Balitora* of the Eastern Himalayas and the hills of Assam is found nowhere else in India except in the Western Ghats where it seems to have proliferated into two other genera, *Bhavania* Hora and *Travancoria* Hora. *Bhavania*, though belonging to the Homalopterinae, possesses small gill-openings above the bases of the pectoral fin, a modification paralleled only among certain genera of the Gastromyzoninae.

Two Plausible Explanations of Fish Dispersal

In their evaluation of zoo-geographica data, geologists have, as a rule, attached little importance to the distribution of

[1] Hora, S. L., *Mem. Ind. Mus.*, XII, pp. 263-330 (1932).

freshwater fishes, for they believe that the ova of freshwater fishes and other animals inhabiting lakes and rivers are capable of being carried alive from one piece of water to another by some natural agency. Among the natural agencies are included wading birds and met orological phenomena. Wading birds may carry eggs in mud sticking to their legs but in the rocky streams there are no wading birds nor there is any mud with which the eggs could stick. The hill-stream birds of the Eastern Himalayas are generally small and they feed on insects. Their distribution is limited by altitudinal factors also.

For instance, take "The White-capped Redstart" (*Chaimarrornis leucocephala*), which is essentiallya bird of rivers and streams and is seldom found away from them. It feeds principally on insects and its range extends from Afghanistan, Baluchistan and Gilgit to extreme eastern Assam and thence to Northern Shan States and Yunnan. During winter, they may come down to the foot-hills but during summer they wander upto about 18,000 feet.

The Plumbeous Redstart (*Rhyacornis fuliginosa*) also keeps entirely to the beds of streams and rivers and is a very active bird. When perched on a convenient stone in the middle of a stream it constantly flickers its tail. It feeds on insects and is found all along the Himalayas. Its range extends to Northern Burma, Northern Siam, Yunnan, and Central and South China and Hainan.

The Himalayan Whistling Thrush (*Myophonus coeruleus*) is also a Himalayan bird co-extensive in its range of distribution with the other two species. It feeds on worms and other organisms in the streams and in wet bush-forest.

The Little Forktail (*Microcichla scouleri*) haunts the most turbulent of small hill-streams and is rarely found in the plains. It is also a Himalayan bird, the range of which extends eastwards to the hills of Northern Burma.

From the habits, habitats and distribution, both altitudinal and geographical, of these or such other Himalayan hill-stream

birds, it can be reasonably inferred that they cannot possibly act as an agency for the dispersal of hill-stream fishes between the Eastern Himalayas on the one hand and the Western Ghats on the other.

Violent cyclonic storms could, no doubt, catch up not only eggs and larvae but also adult fish and drop them at a considerable distance as "rain of fishes". This is true of lake and pond fishes, but in the case of the Homalopteridae their habitat is not conducive to their being lifted in the air and transported over long distances. Secondly, the path of the cyclonic storms is not from the Eastern Himalayas to the Western Ghats and in any case the long distance between the two places should mitigate the possibility of such a means of dispersal.

Palaeogeographical Significance of the Distribution of the Indian Homalopteridae.

We have seen that no natural agency could account for the remarkable distribution of the Homalopteridae in Indian waters and particularly the occurrence of the same species of *Balitora* both in the Assam hills, Eastern Himalayas and Burma on the one hand and the Western Ghats on the other. How could then these forms migrate to the Western Ghats is a palaeogeographical problem which I shall now endeavour to elucidate.

If you look at the structural map of India, you will notice that India proper is composed of three distinct units which differ greatly both in their physical features and geological history. The first division comprises the triangular plateau of the Peninsula, including the island of Ceylon; it has mostly been a land area ever since the Cambrian period. The second division consists of the mountain region, which forms the boundary of India on the north-west, the north and the north-east; it is known as the Extra-Peninsular India. This region was under the sea for the greater part of its history and became dry land probably during the Tertiary period. The third geological division of India comprises the great Indo-Gangetic Plain which separates the Peninsula from

Extra-Peninsular India ; it extends from the valley of the Indus in Sind to that of the Brahmaputra in Assam. Its formation is attributed to the orogenic movements that resulted in the uplift of the Himalayas into a mighty mountain range ; for it is believed that this area in the pre-Tertiary or early Tertiary periods formed a part of the Peninsula. A chip of the Peninsular block is still represented to the east of the Ganges in the Assam Hills.

Hypotheses and Conclusions

Without going into the detailed history of various events that have given to the present-day India its existing structure, I shall refer to certain physiographic features of India which have a special bearing on the subject matter of my talk.

From the structural map of India, it is obvious that the Assam hills must have been continuous with and once formed a part of Peninsular India. When did the gap between the Garo hills and the Rajmahal hills make its appearance is still a matter of controversy among geologists but if the distribution of torrential fishes is any criterion for such a study, the gap would appear to be a very recent structure. Let the geologists and geographers re-examine their data and see how far they support the view I have advanced recently.[1]

The second point on which geologists, geographers and I are happily in agreement concerns the Satpura-Vindhyan trend of mountains stretching from the Assam Himalayas in the east to the Gujarat portion of the Western Ghats in the west. The Satpuras, though low and greatly weathered now, formed the backbone of, geologically speaking, ancient India and I believe their importance diminished *pari passu* with the rise of the Himalayas. If the Garo-Rajmahal Gap is a recent feature of the physiography of India, it will have also to be conceded that the Satpuras formed a fairly high continuous range of mountains upto very recent times. As I shall show presently, both the absence of the gap and the

[1] Hora, S. L., *Proc. Nat. Inst. Sci. India*, X, pp. 423-439 (1944).

grandeur of the Satpuras are essential pre-requisites for the movements of the Eastern Himalayan fishes to the Western Ghats.

The third point which I want to make out is that at some stage in the rise of the Himalayas, a barrier occurred somewhere in the Nepal Himalayas which stopped the migration of eastern fauna to the west and deflected the same over the Assam hills and the Satpuras to the Western Ghats. This means that such earth movements were produced which tended to deflect the rivers of the north-east to the south-west. In his account of "The Evolution of the River system of South Eastern Asia," Gregory[1] has shown that probably from the Quaternary to the Recent periods there were series of extensive river-captures, in which, as a rule, the rivers on the west beheaded the rivers on the east thus transferring bodily the fauna of the latter into that of the former but not in the reverse direction.

The last point I wish to refer is about Peninsular India. This stable land-mass also seems to have undergone some changes during, comparatively speaking, recent times. Separation of Ceylon from India and the sinking of a part of the Peninsula towards the west are evidences of movements which tended to deflect the fauna of the Western Ghats to the south and west as the land-mass was sinking in those directions.

By combining these four hypotheses, we can draw the following conclusions with regard to the changes in the physical features of India. From the Quaternary to the Recent period, the Vindhyas and the Satpuras still formed a continuous and fairly elevated mountain range across India stretching from the Assam Himalayas to the Western Ghats and that the Garo-Rajmahal Gap was non-existent then. During this period such orogenic movements occured which resulted in a series of river captures in which the north-eastern hill-stream fauna was deflected over the Satpura trend to the Western Ghats and thence to the

[1] Gregory, J. W., *Scottish Geog. Mag.*, XLI, pp. 129-141 (1925).

extreme south. Besides the Homalopteridae, to which reference has already been made, there is a large number of other hill-stream fishes, the distribution of which also leads to the same conclusion.

A close study of the fish fauna of the Western Ghats has revealed that deflection of fishes from the east to the west was accomplished in a series of steps or waves of migration. The first wave occured when Ceylon still formed a part of India, the second wave occured before the formation of the Palghat Gap, the third just before the final phase of the Deccan Traps, a fourth after the formation of the Deccan Traps and one wave did not reach the Western Ghats. In the distribution of fishes there is evidence of at least five waves of migration before the Garo-Rajmahal Gap appeared and it would thus seem to be a very recent feature in the physiography of India. Further, it would appear that the final phase of the Deccan Traps most probably occurred in more recent times than the Tertiary, for the fish remains collected from the Intertrappean beds[1] show evidence of the existence of modern fish fauna at that period.

In the light of what I have stated above, may I suggest to the Indian geologists and geographers to re-examine their data with regard to the following features of the physical geography of India :—

1. The age of the Garo-Rajmahal Gap.
2. The age of the Ganges and the Son Rivers.
3. The age of Ceylon as an isolated island.
4. The age of the Palghat Gap.
5. The age of the final eruptions of Deccan Trap.

From the evidence afforded by the distribution of torrential fishes, it seems most probable that all these features are not older than the Quaternary period of the earth's history.

[1] Hora, S. L., *Rec. Geol. Surv. Ind.*, 73, pp. 267-294, (1938).

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THE DISTRIBUTION OF CROCODILES AND CHELONIANS IN CEYLON, INDIA, BURMA AND FARTHER EAST.

By SUNDER LAL HORA, *D.Sc., F.R.S.E., F.Z.S., F.R.A.S.B., F.N.I., Director, Zoological Survey of India, Banaras.*

(*Re*　　*ril 12; read May 4, 1948.*)

CONTENTS.

INTRODUCTION.

In 1901, the completion of the Vertebrata in the *Fauna of British India* afforded an opportunity to Blanford to review and discuss the distribution of vertebrate animals throughout Ceylon, India and Burma. His object was 'to determine the divisions into which the Indian Empire can be classed by our present knowledge of the Vertebrata, and especially to ascertain the zoological relations between the Indian Peninsula and the neighbouring countries'. To achieve this object, he reviewed the distribution of genera, for 'families and sub-families alone being too few in number and ranging in general over wider tracts than genera do, so that it is difficult to determine subregional divisions by means of them, whilst species are too numerous and too unequal in importance'. For some years I have been interested in the distribution of freshwater fishes throughout south-eastern Asia and in the revision of genera characteristic of mountainous regions. My views and conclusions based on these studies are given in the article 'On the Malayan Affinities of the Freshwater Fish Fauna of Peninsular India, and its bearing on the probable age of the Garo-Rajmahal Gap' (Hora, 1944). In the discussion that followed the reading of this paper, the views of some of the leading Indian geologists on the Garo-Rajmahal Gap are given and there is considerable wealth in their observations regarding some palaeogeographical features of India. In the course of these studies it has become abundantly clear to me that the distribution of some of the genera, as given by Blanford, has proved to be erroneous due to incorrect determinations and that this fact has greatly vitiated the value of his work, monumental and outstanding as it is and will always remain, for our present-day studies. The revision of the *Fauna* volumes on certain groups of Vertebrata, therefore, affords another opportunity to review the distribution of Indian fauna and to elucidate the zoological relations of the various subregions of India and their relationships with the neighbouring countries. The present article is written with this object in view.

As the revised editions of the *Fauna* volumes dealing with Batrachia and Fishes have not yet been published, a complete revision of Blanford's article is not possible at the present time, but sufficient information is available regarding the distribution of Mammals, Birds, Reptiles, and certain families of fishes to warrant the publication of some articles. It will at least serve to obtain the views of other zoologists interested in similar studies.

Besides correct and reliable determination of animals, it is equally essential for zoogeographical studies that the ecological factors influencing the lives of different groups of animals should also be known, for knowledge of an animal without some knowledge of its environment is very imperfect indeed. In studying the zoogeography of the mountainous fishes, I had a great advantage in knowing something about the ecology, bionomics and evolution of the torrential fauna (Hora, 1930). The revised edition of the Vertebrata in the *Fauna* are in this respect a great improvement on the earlier volumes, for they contain not only the systematic descriptions of the species but also notes on their habits and habitats.

Though families and sub-families are generally unsuitable for zoogeographical studies, the same may be said of genera to a lesser extent, for species, however unequal in value, are our units of study. Whether we catalogue them or not, it is necessary to keep them in mind always. For the first article of the series, I have, therefore, selected the groups of Crocodiles and Chelonians as the number of species to be dealt with is not large. Besides, the volumes on Reptiles cover a much larger geographical area, as they include the whole of the Indo-Chinese Peninsula. In support of this departure from the usual practice, Smith (1931, p. 13) states that 'The fauna of Siam, French Indo-China and southern China is so closely allied to that of Burma that it would be scientifically incorrect to separate them from one another'. This is true of other groups of animals also. Not only is the fauna of Burma closely allied to that of Siam, French Indo-China and southern China but the same can be said with regard to the fauna of the Eastern Himalayas and the Malabar Tract of the Western Ghats.

For the present series of articles on Reptiles, I have retained the two subregions proposed by Smith and the twelve zoogeographical areas into which he has divided them. The distribution of various species as tabulated below has been checked by Dr. Malcolm A. Smith. I am grateful to him for this.

The geographical limits of the twelve areas, as recognized by Smith, are given below for convenience of reference.

ZOOGEOGRAPHICAL AREAS.

The Oriental Region is divided into three Subregions, the Indian, the Indo-Chinese and the Malaysian. The Indian Subregion includes the peninsula of India as far east as Bengal at about longitude 90° and south of the Himalaya Mountains. It has been divided into seven geographical areas as follows:—

1. *The Desert Area of North-West India.*—This includes Baluchistan, the North-West Frontier Province, the Punjab, Western Rajputana as far as the Aravalli Range and Sind.

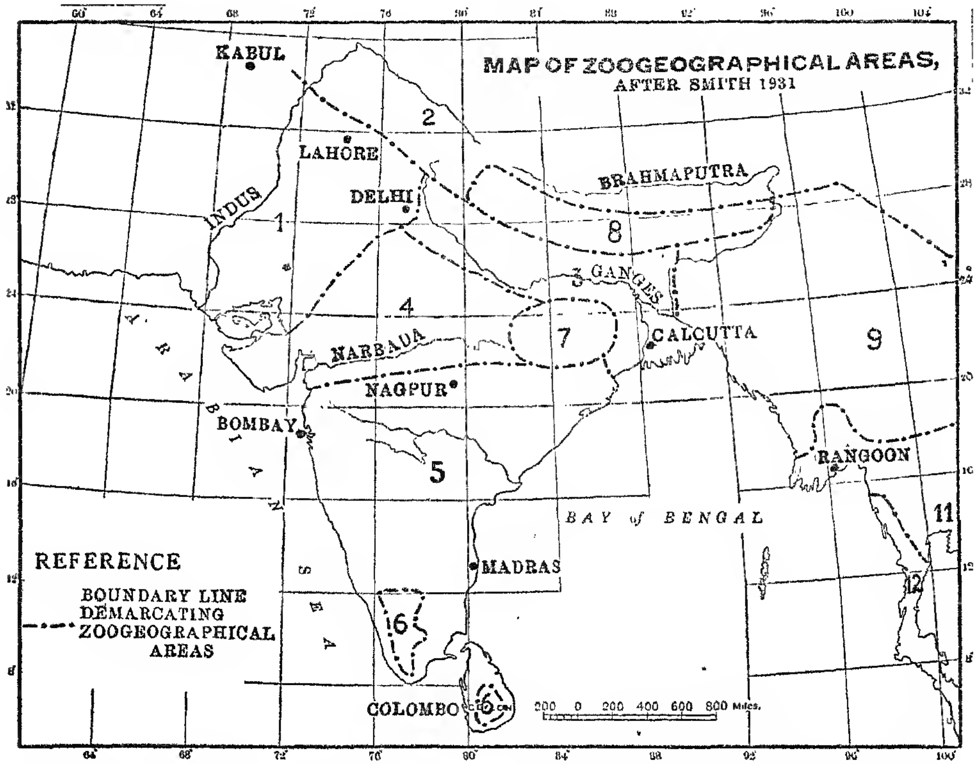
2. *Kashmir and the Western Himalayas up to Nepal.*—Most of the country is mountainous and highly elevated.

3. *The Gangetic Plain.*—The great Gangetic Plain of Northern India extends from the Valley of the Indus in Sind to the right bank of the Brahmaputra in Bengal.

4. *Central India.*—This includes the area between the Gangetic Plain, the Deccan, the Aravalli range and Chota Nagpur.

5. *The Deccan.*—This includes the central tableland of the Deccan between 12° and 21° north latitude. A part of the Western Ghats is included in this area.

6. *The Mountains of the Malabar Tract and Ceylon.* The hills of the Peninsula south of lat. 12°N. together with the mountains of Ceylon constitute a distinct faunal region.



TEXT-FIG. 1. Map of the Zoogeographical Areas of India, Ceylon and Farther East as recognised by Dr. M. A. Smith in the revised edition of the *Fauna of British India* on Reptilia.

7. *The Chota Nagpur Area.*—This includes Bihar south of the Gangetic Plain, the northern part of Orissa, and the eastern part of the Central Provinces.

Comparing the above zoogeographical divisions with those proposed by Blanford, it will be seen that there is considerable general agreement between the two systems as is shown below:—

Smith's Classification.	*Blanford's Classification.*
The Desert Area of N.W. India.	Punjab Tract, excluding the plain of the Indus.
Kashmir and the Western Himalayas.	Western Himalayan Tract.
The Gangetic Plain.	North-Western Provinces (now designated as the United Province and Bihar) Tract including the plain of tho Indus *plus* Bengal Tract.
Central India.	Rajputana or Central Indian Tract.
The Deccan.	Carnatic or Madras Tract.
The Mountains of the Malabar Tract and Ceylon.	Malabar Coast Tract and Ceylon Tract.
The Chota Nagpur Area.	Bihar Orissa Tract.

Judging from the distribution of freshwater fishes, Smith's classification would seem to be a better arrangement of the zoogeographical areas into which India west of the Brahmaputra in Bengal can be divided.

Smith has divided his Indo-Chinese Subregion into 5 areas, namely,—

1. *The Eastern Himalayas.*—which corresponds with the Assam Tract of Blanford, and extends from the western frontier of Nepal to the termination of the range at the bend of the Brahmaputra.
2. *The Trans-Himalayan Mountainous Area* [1].—corresponds to the Upper Burma Tract of Blanford and includes the hills of Assam east of the Brahmaputra, the whole of Burma, except the lowlands in the south, southern Yunnan, the northern part of French Indo-China and the northern part of Siam.
3. *Annam.*
4. *The Great Plain of Indo-China.*—This area includes the lowlands of Burma south of Prome and Toungoo and at the mouth of the Salween, the great plains of Siam, Cambodia, and Cochin China. This corresponds to the Pegu Tract of Blanford.
5. *Tenasserim and Peninsular Siam.*—This area corresponds to the Tenasserim and South Tenasserim Tracts of Blanford and includes the mountain chain which extends down the peninsula.

Ecological Factors influencing Animal Life in Various Zoogeographical Areas.

In a recent article, of which I have seen a summary in English, Nikolsky (1947) has discussed biological peculiarities of faunistic complexes and the value of their analysis for zoogeographical studies. He has rightly pointed out that 'A zoogeographical division into definite regions is a stage which belongs chiefly to the past, being now nearly completed with regard to large areas'. In his opinion, with which I agree, 'The criterion on the ground of which a certain species is referable to one or another faunistic complex besides the character of a distribution area is its ecological specificity, *i.e.* its relation to both abiotic and biotic media which are closely connected with each other, being both a sequence of the adaptation to life in a definite geographical zone'. From the above, it will follow as a natural sequence that 'In populating a new basin the members of a faunistic complex occupy its part the conditions of which approach most the zone where the formation of the complex has proceeded'. It will, therefore, be clear that in elucidating the history of the origin of the fauna, its ways of distribution, its interrelations with other zoogeographical areas, etc., etc., it is absolutely necessary to bear in mind the biological peculiarities of the fauna and the principal factors in its environment. Evolution is the result of the action and reaction of these important conditions which govern the life of an animal and determine its survival, modification or annihilation under changed conditions of environment, if any.

Before discussing the distribution of Crocodiles and Chelonians, it will be advantageous, therefore, to bear in mind the main ecological conditions which affect the fauna in the twelve zoogeographical areas enumerated above.

The Desert Area of North-West India is desert or semi-desert, except near the rivers. The rainfall averages from nil in certain portions to 20 inches in the year in others. The interior of Baluchistan is from 3,000 to 6,000 feet above sea-level.

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[1] It may be pointed out that among geographers the term Trans-Himalaya has a definite meaning and generally signifies the high plateau of Central Asia to the north of the Himalayas.

The fauna exhibits some interesting adaptive modifications to withstand extreme heat and drought.

In the *Kashmir and the Western Himalayan Areas*, the country is mountainous and highly elevated. *The Gangetic Plain* is divisible into a western, more or less arid or semi-arid area and an eastern area with a fertile, alluvial soil which is cleared, cultivated and thickly populated for the most part. The rainfall is 20 to 30 inches in the western portion and 50 to 100 inches in the eastern region.

The Central India is an undulating and hilly tract cleared and cultivated in parts and covered with brushwood or thin forest of small trees. The average rainfall is about 35 inches. *The Deccan Area* is similar to the Central India but the rainfall along the western coast is heavy—from 100 to 200 inches annually. The Eastern Ghats have not the same unity of structure as the Western Ghats and represent a discontinuous line of mountain country. *The mountains of the Malabar Tract and Ceylon* rise to a considerable height and most of the area is well forested. The rainfall is heavy, between 90 and 150 inches, and owing to its approximation to the equator, seasonal changes are not so marked. *The Chota Nagpur Area* is hilly and, with a few exceptions, is heavily forested. The average rainfall is between 50 to 70 inches in the year. The highest peak in the Chota Nagpur area is the Parasnath Hills, 4,800 feet above sea-level.

The Eastern Himalayas are sub-tropical and heavily forested. The average rainfall is 50 to 150 inches. *The Trans-Himalayan Mountainous Area* is of hills and dense forests closely resembling the Eastern Himalayas. The rainfall is heavy, generally exceeding 100 inches annually over a considerable part of the area. *The Tenasserim and the Peninsular Siam Area* is also mountainous and heavily forested, with the yearly average rainfall being 150 to 200 inches. *Annam* is entirely mountainous and the conditions are similar to those of Burma. *The Great Plain of Indo-China* is for the most part flat, alluvial and more or less cultivated and populated. The annual rainfall in the Pegu area is from 100 to 125 inches, in Bangkok it is 55, in Cochin China 50 to 90 inches.

In the case of aquatic forms, continuity of water courses is essential at some period of the earth's history for their dispersal and for the dispersal of land animals, temperature, humidity and vegetation are the chief governing factors. Continuity of land-masses is also an essential factor in the distribution of torrential forms. Crocodiles and Chelonians could only be distributed over wide areas through natural agencies. For the survival of a species in a new geographical area after its dispersal, it is important that similar ecological conditions in its new habitat must persist, otherwise it will have to undergo some sort of modifications to adapt itself to new conditions. Such modifications will, of course, depend on the intensity of variation within the species itself under the new environmental conditions and the resulting animal will either become a geographical race, form, subspecies or a new species. Even new genera and families may result from long isolation or some kind of habitudinal segregation.

Ecologically speaking, it will thus be seen that, with the exception of the Plain of Indo-China, the remaining four areas of the Indo-Chinese Subregion are very closely allied to the Malabar Tract and Ceylon and also resemble the Western Ghats and the Chota Nagpur plateau. It is no wonder, therefore, that in the migration of the fauna and the development of the present-day features of India's physical geography, pockets are formed where similar or identical species could continue to live undisturbed under environmental conditions more or less similar to those under which they had once lived over a much wider area. We shall refer to these points again when dealing with certain aspects of the palaeogeography of India, but now we may consider the distribution of the Crocodiles and Chelonian listed by Smith from the Indian and the Indo-Chinese Subregions.

THE DISTRIBUTION OF CROCODILES AND CHELONIANS IN CEYLON, INDIA, BURMA AND FARTHER EAST.

Zoogeographical Areas of Greater India based on the Distribution of Reptiles (After Smith).

Families, Genera and Species	The Indian Subregion							The Indo-Chinese Subregion					*Distribution and general remarks*
	1	2	3	4	5	6	7	8	9	10	11	12	
Family CROCODILIDAE Gray ..	..	..	..	..	..	..	..	..	..	..	..	..	Southern Asia; the East Indian Archipelago and tropical Australian region; Africa; tropical and subtropical America.
Genus *Gavialis* Oppel. ..	..	..	..	..	..	..	..	..	..	..	..	..	Occurs in the Pliocene deposits of the Siwalik Hills and Narbada valley.
1. *Gavialis gangeticus* (Gmelin). ..	x	..	x	..	..	..	..	..	x	..	..	..	The Indus, Ganges, Brahmaputra Rivers and their tributaries, and the Kaladan River, Arakan.
Genus *Crocodilus* Gronovius													
2. *Crocodilus porosus* Schneider. ..	..	..	..	..	..	..	..	..	..	..	..	..	The Estuarine Crocodile inhabits the mouths of muddy rivers and canals near the sea.
3. *Crocodilus siamensis* Schneider. ..	..	..	..	..	..	..	..	..	..	..	x	x	Siam; French Indo-China; the Malay Peninsula; Java.
4. *Crocodilus palustris* ..	x	x	x	x	x	x	x	?	..	..	..	..	India and Ceylon.
Family SPHARGIDAE Gray													
Genus *Dermochelys* Blainville													
5. *Dermochelys coriacea* (Linn.)	..	..	..	..	..	..	..	..	..	..	..	..	Marine.

1. The Desert Area of North-West India. 2. Kashmir and the Western Himalayas. 3. The Gangetic Plain. 4. Central India. 5. The Deccan. 6. The Mountains of the Malabar Tract and Ceylon. 7. The Chota Nagpur Area. 8. The Eastern Himalayas. 9. The Trans-Himalayan Mountain Area. 10. Annam. 11. The Great Plain of Indo-China. 12. Tenasserim.

Families, Genera and Species	The Indian Subregion							The Indo-Chinese Subregion					Distribution and general remarks
	1	2	3	4	5	6	7	8	9	10	11	12	
Family CHELONIDAE Gray													
Genus *Eretmochelys* Fitzinger													
6. *Eretmochelys imbricata* (Linn.)	..	..	..	..	..	..	..	..	..	..	..	..	Marine.
Genus *Chelonia* Brongniart													
7. *Chelonia mydas* (Linn.)..	..	..	..	..	..	..	..	..	..	..	..	..	Marine.
Genus *Caretta* Refinesque													
8. *Caretta caretta olivacea* (Eschscholtz).	..	..	..	..	..	..	..	..	..	..	..	..	Marine.
Family PLATYSTERNIDAE Gray													
Genus *Platysternum* Gray													
9. *Platysternum megacephalum* Gray.	..	..	..	..	..	..	..	..	x	..	x	x	Southern Burma; Siam; French Indo-China; Southern China; Hainan.
Family EMYDIDAE Gray													
Genus *Cyclemys* Bell.													
10. *Cyclemys mouhoti* Gray	..	..	..	..	..	..	..	x	x	..	x	..	Assam; French Indo-China and Hainan.
11. *Cyclemys dentata* Gray	..	..	..	..	..	..	..	x	x	x	x	x	Assam Hills, Burma, French Indo-China, Annam, the Malay Peninsula and Archipelago and Philippine Islands.

Families, Genera and Species	The Indian Subregion							The Indo-Chinese Subregion					Distribution and general remarks
	1	2	3	4	5	6	7	8	9	10	11	12	
Family EMYDIDAE Gray—*contd.*													
12. *Cyclemys annamensis* Siebenrock.	..	..	..	..	..	..	..	..	..	x	..	..	Annam.
Genus *Cuora* Gray													
13. *Cuora amboinensis* (Daudin).	..	..	..	..	..	..	..	..	..	..	x	x	Tenasserim; Siam; Cambodia; Cochin China; the Malay Archipelago and Peninsula; the Philippine Islands.
14. *Cuora flavomarginata* (Gray).	..	..	..	..	..	..	..	..	x	..	..	..	Southern China; Formosa; the Lu Chu Islands.
15. *Cuora trifasciata* (Bell)	..	..	..	..	..	..	..	..	x	..	..	..	Southern China; Hainan.
16. *Cuora yunnanensis* (Blgr.)	..	..	..	..	..	..	..	..	x	x	..	..	Yunnan Fu and Tong Chuan Fu.
Genus *Geoemyda* Gray													
17. *Geoemyda spengleri* (Gmelin).	..	..	..	..	..	..	..	..	x	x	..	x	Southern China; Annam; the Malay Archipelago; Japan.
18. *Geoemyda spinosa* Bell	..	..	..	..	..	..	..	..	..	..	x	x	Tenasserim; Peninsular Siam; the Malay Peninsula; Sumatra, Borneo; Natuna Islands.
19. *Geoemyda silvatica* (Henderson).	..	..	..	..	x	..	..	..	..	..	..	..	Cochin.
20. *Geoemyda depressa* (Anderson).	..	..	..	..	..	..	..	..	x	..	..	..	Arakan Hills.
21. *Geoemyda tricarinata* (Blyth).	..	..	..	..	..	..	x	x	..	..	..	..	Chota Nagpur; North Bengal; North Assam.

Families, Genera and Species	The Indian Subregion							The Indo-Chinese Subregion					Distribution and general remarks
	1	2	3	4	5	6	7	8	9	10	11	12	
Family EMYDIDAE Gray—*contd.*													
22. *Geoemyda trijuga* (Schweigger).	..	..	..	..	x	x	x	x	x	..	..	..	*trijuga* (forma typica), Bombay; Madras; Mysore State. *trijuga edeniana*, Burma. *trijuga indopeninsularis*, Chota Nagpur. *trijuga coronata*, Travancore and Cochin. *trijuga thermalis*, Ramnad and Ceylon.
23. *Geoemyda grandis* Gray	..	..	..	..	..	..	..	..	x	..	x	x	Burma; Siam; Cambodia; the Malay Peninsula.
Genus *Damonia* Gray													
24. *Damonia subtrijuga* (Schlego & Müll.).	..	..	..	..	..	..	..	..	..	..	x	x	Siam; Cochin-China; Northern Malay Peninsula; Java.
Genus *Hieremys* Boulenger													
25. *Hieremys annandalei* (Blgr.).	..	..	..	..	..	..	..	..	..	..	x	x	Central Siam; Cambodia; N. Malay Peninsula.
Genus *Notochelys* Gray													
26. *Notochelys platynota* (Gray).	..	..	..	..	..	..	..	..	..	..	x	x	Cochin-China; the Malay Peninsula and Archipelago.
Genus *Geoclemys* Gray													
27. *Geoclemys hamiltoni* (Gray).	x	..	x	..	..	..	..	..	..	..	..	..	Northern India from Sind to Bengal.
Genus *Siebenrockiella* Lindholm													

Families, Genera and Species	The Indian Subregion							The Indo-Chinese Subregion					Distribution and general remarks
	1	2	3	4	5	6	7	8	9	10	11	12	
Family EMYDIDAE Gray—*contd.*													
28. *Siebenrockiella crassicollis* (Gray).	..	..	..	..	..	..	..	..	..	..	x	x	Tenasserim; Siam; Cochin-China; the Malay Peninsula and Archipelago.
Genus *Clemmys* Ritgen													
29. *Clemmys mutica* (Cantor)	..	..	..	..	..	..	..	..	x	..	..	..	Southern China; Formosa; Hainan.
30. *Clemmys bealei* (Gray)	..	..	..	..	..	..	..	..	x	x	..	..	Southern China; Northern Annam; Hainan.
Genus *Chinemys* Smith													
31. *Chinemys reevesi* (Gray)	..	..	..	..	..	..	..	..	x	..	..	..	Yunnan; S.E. China to Japan.
Genus *Ocadia* Gray													
32. *Ocadia sinensis* (Gray)	..	..	..	..	..	..	..	..	x	x	..	..	Southern China; Formosa; Hainan; Annam.
Genus *Morenia* Gray													
33. *Morenia ocellata* (Dum. & Bib.).	..	..	..	..	..	..	..	..	x	..	..	x	Southern Burma and Tenasserim.
34. *Morenia petersi* Anderson	..	..	x	..	..	..	..	..	..	..	..	..	Bengal.
Genus *Hardella* Gray													
35. *Hardella thurgi* (Gray)	..	..	x	..	..	..	..	..	..	..	..	..	The Gangetic and Brahmaputra River Systems.
Genus *Kachuga* Gray ..	..	..	..	..	..	..	..	..	..	..	..	..	Fossils in the Pleistocene of the Siwalik Hills and the Narbada Valley.
36. *Kachuga smithi* (Gray)	x	..	x	..	..	..	..	..	..	..	..	..	The Indus and the Ganges River Systems.

Families, Genera and Species	The Indian Subregion							The Indo-Chinese Subregion					Distribution and general remarks
	1	2	3	4	5	6	7	8	9	10	11	12	
Family EMYDIDAE Gray—*concld.*													
37. *Kachuga tectum* (Gray)	x	..	x	..	x	..	..	..	..	..	..	..	*tectum* (forma typica), the Indus, Ganges and Brahmaputra River Systems.
													tectum tentoria; the Mahanadi, Godavari and probably Kistna River Systems.
38. *Kachuga sylhetensis* (Jerdon).	..	..	..	..	..	..	..	x	..	..	..	..	Garo, Khasi and Naga Hills, Assam.
39. *Kachuga dhongoka* (Gray)	..	..	x	..	..	..	..	x	..	..	..	..	N.E. India; the Ganges as far west as Allahabad and north to Nepal. Fossils in the Siwalik Hills.
40. *Kachuga kachuga* (Gray)	..	..	x	..	..	..	..	..	..	..	..	..	The Gangetic River System.
41. *Kachuga trivitta* (Dum. & Bib.).	..	..	..	..	..	..	..	..	x	..	..	..	Burma.
Genus *Batagur* (Gray)													
42. *Batagur baska* (Gray) ..	..	..	x	..	..	..	..	..	x	..	x	x	Bengal, Burma to Cochin-China and the Malay Peninsula; Sumatra.
Family TESTUDINIDAE Gray													
Genus *Testudo* Linneaus													
43. *Testudo elegans* Schoepff.	x	..	..	x	x	x	..	..	..	..	..	..	Throughout Central and Southern India, extending west as far as Sind and south to Ceylon.
44. *Testudo platynota* Blyth	..	..	..	..	..	..	..	..	x	..	..	..	Burma as far south as Moulmein.

2

Families, Genera and Species	The Indian Subregion							The Indo-Chinese Subregion					Distribution and general remarks
	1	2	3	4	5	6	7	8	9	10	11	12	
Family TESTUDINIDAE Gray—*concld.*													
45. *Testudo elongata* Blyth	..	..	..	..	..	..	x	x	x	x	..	x	North-eastern India to Tonkin and the Malay Peninsula as far south as Penang.
46. *Testudo travancorica* Blgr.	..	..	..	..	..	x	..	..	..	..	..	..	Travancore, Cochin and Coorg.
47. *Testudo emys* Schleg. & Müll.	..	..	..	..	..	..	..	x	x	..	x	x	Cachar and Naga Hills, Assam; Burma; Siam; the Malay Peninsula and the Archipelago.
48. *Testudo impressa* (Günther).	..	..	..	..	..	..	..	..	x	x	x	x	Burma; Siam; Annam; Tonkin, the Malay Peninsula.
49. *Testudo horsfieldi* Gray	x	..	..	..	..	..	..	..	..	..	..	..	The Caspian and Aral Seas to the north-western corner of British India.
Family TRIONYCHIDAE Gray ..	..	..	..	..	..	..	..	..	..	..	..	..	Fossil *Trionyx*, *Chitra*, and *Lissemys* indistinguishable from present-day forms have been found in the Pliocene and Pleistocene of the Siwalik Hills of India.
Genus *Lissemys* Smith													
50. *Lissemys punctata* (Bonnaterre).	x	..	x	x	x	x	..	..	x	..	..	..	*punctata* (forma typica), the Indus and the Ganges river systems. *punctata granosa*, the Indian Peninsula south of the Ganges, and Ceylon. *punctata scutata*, the Irrawaddy and Salween rivers.
Genus *Pelochelys* Gray													
51. *Pelochelys bibroni* (Owen)	..	..	..	..	..	..	..	..	x	..	x	?	? Bengal: the Indo-Chinese Peninsula and Southern China; Hainan: ? the Malay Peninsula, Sumatra, Borneo; the Philippine Islands; New Guinea.

Families, Genera and Species	The Indian Subregion							The Indo-Chinese Subregion					Distribution and general remarks
	1	2	3	4	5	6	7	8	9	10	11	12	
Family TRIONYCHIDAE Gray (*contd.*)													
Genus *Chitra* Gray													
52. *Chitra indica* (Gray)	x	x	x	..	..	..	..	x	x	..	x	x	Northern India; Siam; the Malay Peninsula.
Genus *Dogania* Gray													
53. *Dogania subplana* (Geoffrey).	..	..	..	..	..	..	..	..	x	..	x	x	Burma; Siam; the Malay Peninsula and Archipelago; the Philippine Islands; Asia, Africa and North America.
Genus *Trionyx* Geoffrey													
54. *Trionyx gangeticus* Cuvier.	x	..	x	..	x	..	..	..	..	..	..	..	The Indus, Ganges and Mahanadi River Systems.
55. *Trionyx nigricans* Anderson.	..	..	..	..	..	..	..	..	x	..	..	..	Chittagong.
56. *Trionyx leithi* Gray	..	..	x	..	x	..	..	..	..	..	..	..	The Ganges and rivers of Peninsular India as far south as Madras.
57. *Trionyx hurum* Gray	..	..	x	..	..	..	..	..	..	..	..	..	Lower reaches of the Ganges and Brahmaputra.
58. *Trionyx formosus* Gray	..	..	..	..	..	..	..	..	x	..	..	..	Burma.
59. *Trionyx cartilagineus* (Boddaert).	..	..	..	..	..	..	..	..	..	..	x	x	Southern Burma; Siam; French Indo-China as far north as Tonkin; the Malay Peninsula and Archipelago.
60. *Trionyx sinensis sinensis* Weigmann.	..	..	..	..	..	..	..	..	x	x	x	..	*sinensis* (forma typica), Southern China; Indo-China; Annam; Hainan. *sinensis tuberculatus*; Yunnan, Central China; Formosa.
61. *Trionyx steindachneri* Siebenrock.	..	..	..	..	..	..	..	..	x	x	..	..	Southern China; Tonkin; Annam; Hainan.

Of the 61 species of Crocodiles and Chelonians listed above, one species of Crocodile, *Crocodilus porosus*, is estuarine and rarely enters rivers above tidal limits, and four species of turtles, *Dermochelys coriacea, Eretmochelys imbricata, Chelonia mydas* and *Caretta caretta olivacea*, are marine. These five species are not of any zoogeographical significance.

Of the remaining 56 species, 8 are common to the Indian and Indo-Chinese Subregions, 14 are confined to the Indian Subregion and 34 to the Indo-Chinese Subregion. I shall elucidate the significance of each of these groups separately.

Distribution of the Species Common to the Indian and Indo-Chinese Subregions.

Of the eight species common to the Indian and Indo-Chinese Subregions, the Gharial (*Gavialis gangeticus*) represents one of the most primitive of the living reptiles and is the sole survivor of a large number of species that once lived in South-eastern Asia. Fossil forms of *Gavialis* have been described from the Pliocene deposits of the Siwalik Hills and the Narbada Valley and they are known to have attained a length of 50 to 60 feet. The great antiquity of the crocodiles, as is well known to all students of Zoology, is reflected in their discontinuous distribution in the tropical Australian region, South-eastern Asia, Africa and tropical and subtropical America. Thus they indicate the existence of the Gondwanaland which comprised the lands enumerated above and persisted as a large southern continent till the end of the Cretaceous or the beginning of the Tertiary period. The point of interest is that *G. gangeticus*, a survival of the Indobrahm, has persisted throughout the ages of the later Himalayan earth-movements without undergoing any appreciable change in structure. This is no doubt due to the fact that it lives in sluggish rivers and the ecological condition under which it lives have also persisted as such throughout all these ages.

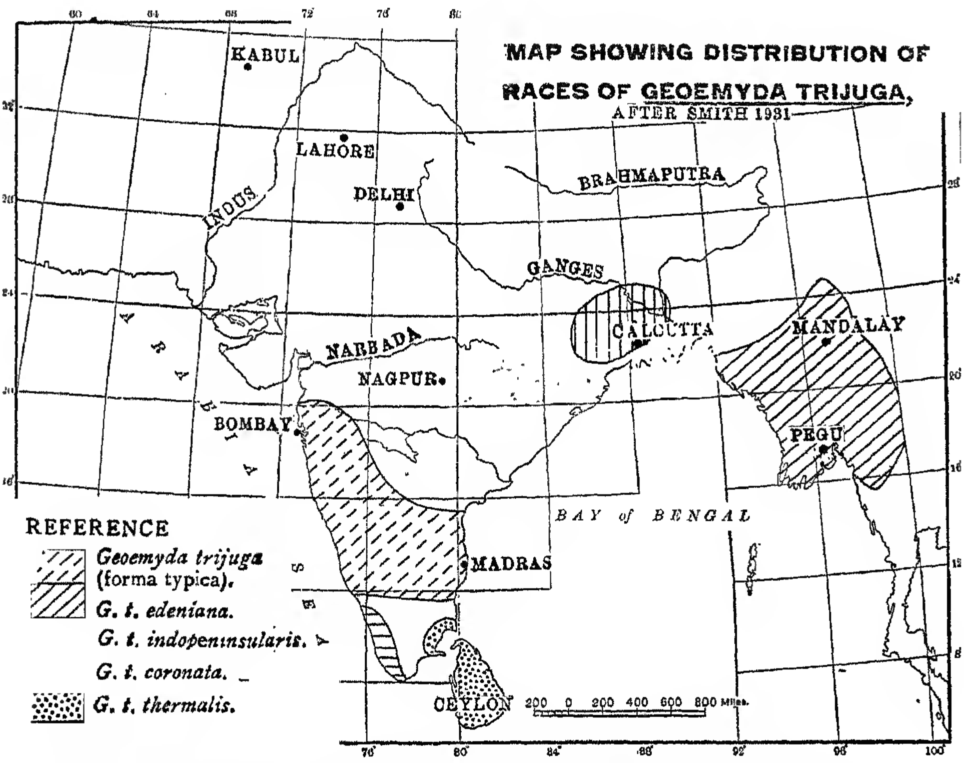
One species of freshwater Tortoise (Terrapins), *Geoemyda trijuga*, and one species of freshwater Turtle (Mud Turtle), *Lissemys punctata*, are of special interest from a zoogeographical point of view as both are found in Burma on the one hand and over a greater part of India on the other. Both have budded out geographical races in different parts of their distribution (Text-fig. 2), no doubt under the varying ecological conditions of their respective habitats.

In the case of *G. trijuga*, a chiefly aquatic and vegetarian species, five fairly well defined races are recognizable, dependent chiefly upon the colouration of the head and to a less extent that of the shell. Variation in colouration is certainly associated with environmental factors and many similar cases are known from among fishes as well. The typical form of the species is known from the Bombay and Madras Presidencies and the State of Mysore; the race *edeniana* from Burma; the race *indopeninsularis* from Chota Nagpur and North Bengal; the race *coronata* from Travancore and Cochin and the race *thermalis* from Ramnad District, Ceylon and the Maldive Islands.[1] The distribution, though extensive, is discontinuous for the Chota Nagpur and North Bengal race is separated from the Bombay race in the west and the Burma race in the east by considerable distances. Geographical isolation and habitudinal segregation may have led to the origin of the present races but there seems hardly any doubt that once *G. trijuga* was uniformly distributed in the intervening portions of its range.

The typical form of the Mud Turtle *Lissemys punctata* is found in the Indus and the Ganges and their tributaries; the race *granosa* is found in the Indian Peninsula

[1] Lt.-Col. R. B. S. Sewell has raised a point regarding the occurrence of this species in the Maldive Islands. Either it is introduced there by human agency or it must have migrated there before the Laccadives and Maldives were separated from India. Personally I favour the latter possibility and feel that such separation occurred not in a very remote geological period.

south of the Ganges while its race *scutata* is found in the Irrawaddy and the Salween Rivers. Its absence from Assam makes its distribution discontinuous but its occurrence in the Indus and the Ganges takes us back to the time of the Indobrahm or the Siwalik River. Though more widely distributed than the Gharial, *Gavialis gangeticus*, it seems to be contemporaneous with it during the Siwalik period.



TEXT-FIG. 2. Map showing the geographical raciation and present-day discontinuous distribution of *Goemyda trijuga* (Schwel.). *After Dr. M. A. Smith.*

The Terrapin, *Batagur baska*, and the Mud Turtle, *Chitra indica*, are essentially Indo-Chinese forms but their range extends into India for a short distance. The former, a herbivorous and entirely aquatic species, is found in Bengal and then its range extends from Burma to Cochin-China and the Malay Peninsula. It is also found in Sumatra. The animal is of exceedingly shy disposition and inhabits estuaries, deep slow flowing rivers and canals. It is likely, therefore, that its distribution to Bengal may have been affected *via* the Bay of Bengal during the monsoons when the salinity near the head of the Bay falls very low.

Chitra indica, on the other hand, feeds upon fish, molluscs and other animal food, and is a very pugnaceous animal. It is found in Northern India, Siam and the Malay Peninsula. It has been recorded from the Irrawaddy also, though this needs confirmation. From its distribution, it appears to be a species of the Indobrahm.

The Land Tortoise, *Testudo elongata*, is found in Chota Nagpur on the one hand and in north-eastern India to Tonkin and the Malay Peninsula on the other. Dr. Annandale had recognised the Chota Nagpur form as a separate species, which he

called *T. parallelus* and remarked on its close resemblance to *T. elongatus*, an Indo-Chinese species.

The Terrapin, *Geomyda tricarinata*, is found in the Chaibasa District of Chota Nagpur on the one hand and Northern Bengal (Jalpaiguri District) and Assam (Daflas Hills and Bisnath Plain) on the other. This herbivorous, aquatic species must have once occurred over the intervening areas in the Vindhya and Satpura trend of mountains.

The Terrapin, *Kachuga dhongoka*, at present occurs in North-east India and in the Ganges as far west as Allahabad and north to Nepal but its fossils are known from the Siwalik Hills. It is, therefore, a species dating back to the Indobrahm when its range must have been more extensive.

Distribution of the Species of the Indian Subregion.

Of the 14 species of Crocodiles and Chelonians, 3 have a very restricted distribution. The Terrapin, *Geoemyda silvatica*, is known only from the forests of the Cochin State and inhabits short burrows underground and does not show any partiality for water. It can live entirely upon vegetable food. The Land Tortoise, *Testudo travancorica*, is known from the hills of Travancore, Cochin and Coorg. This species appears to have been derived from *T. elongata*, the range of which extends from North-east India to Tonkin and the Malay Peninsula as far south as Penang. The endemicity of a large number of species in the Malabar Tract of India and Ceylon and their close affinity with Malayan forms are well known facts and indicate their long isolation from the parent stock leading to the evolution of new species.

The Terrapin, *Morenia petersi*, is restricted to Eastern Bengal (Jessore, Dacca, Fatehgarh) but little is known about its habits or habitat. The Terrapin, *Kachuga kachuga*, is also definitely known from the Gangetic River System.

Another species of somewhat restricted distribution is the Mud Turtle, *Trionyx hurum*, definitely known so far from the lower reaches of the Ganges and the Brahmaputra. The Mud Turtle, *Hardella thurgi*, is found in the Gangetic and Brahmaputra River Systems.

The species that are found in the Indus and the Ganges River Systems are of special interest in so far as they support the view that before the Indus and the Ganges were evolved as present-day rivers, they formed the Indobrahm or the Siwalik River of the Pleistocene period (Pascoe 1919; Pilgrim 1919). The Terrapin, *Geoclemys hamiltoni*, which is represented by fossils in the Siwalik Hills, is at the present day found in Northern India from Sind to Bengal. It is carnivorous in its habits. Another Terrapin, *Kachuga smithi*, is found in the tributaries of the Indus and the Ganges though it is more common in the former river. The Terrapin, *Kachuga tectum*, is represented in India by two geographical races; its typical form is found in the Indus, Ganges and the Brahmaputra River Systems while the race *tentoris* is found in the Mahanadi and the Godavari rivers. Here again we find species in formation through isolation or some form of habitudinal segregation. The Mud Turtle, *Trionyx gangeticus*, is also found in the Indus, Ganges and the Mahanadi River Systems. It is interesting to note that Annandale had recognised the Mahanadi form as a separate race, *mahanaddicus*, though Smith did not agree with Annandale. At any rate, there are some differences in colouration from the typical form and in the Mahanadi, therefore, we have an incipient new species of some future age.

Another Mud Turtle which has spread southwards from the Ganges to the rivers of the Peninsula is *Trionyx leithi* at present known from the Ganges and the rivers of the Peninsula as far south as Madras. This species is closely allied to *T. gangeticus* and is co-extensive with it for a certain part of its range (Ganges and

Mahanadi River Systems). Here we have perhaps an instance of the budding of a new species from the older one of the Indobrahm.

We have so far dealt with the forms associated in one way or the other with the Ganges System, but two species definitely exhibit Western Asiatic affinities. The Starred Tortoise, *Testudo elegans*, is distributed throughout Central and Southern India, extending west as far as Sind and south to Ceylon. Though a forest dweller, it is found in dry areas of the low country. The genus *Testudo* is cosmopolitan in its distribution, except Australia and Papuasia, and it is likely that *T. elegans* is a migrant or descendant of forms living north-west of Sind. Another Land Tortoise, *Testudo horsfieldi*, shows definitely that it is a migrant into India from the Aral and Caspian Seas Regions. It is only found in the north-western corner of India and has not spread further south.

The most widely distributed species of the Indian Region is the Crocodile, *Crocodilus palustris*. It is found in the whole of the Indian Peninsula and Ceylon, extending as far west as the Dasht River near the Persian Frontier, in Baluchistan, north to Nepal and east as far as the Darrang District on the Brahmaputra in Assam.

General Remarks concerning the Indian Subregion.

Before taking up the analysis of the species only known from the Indo-Chinese Subregion, we may briefly summarise the trends of distribution of the forms known from the Indian Subregion. The main points are:—

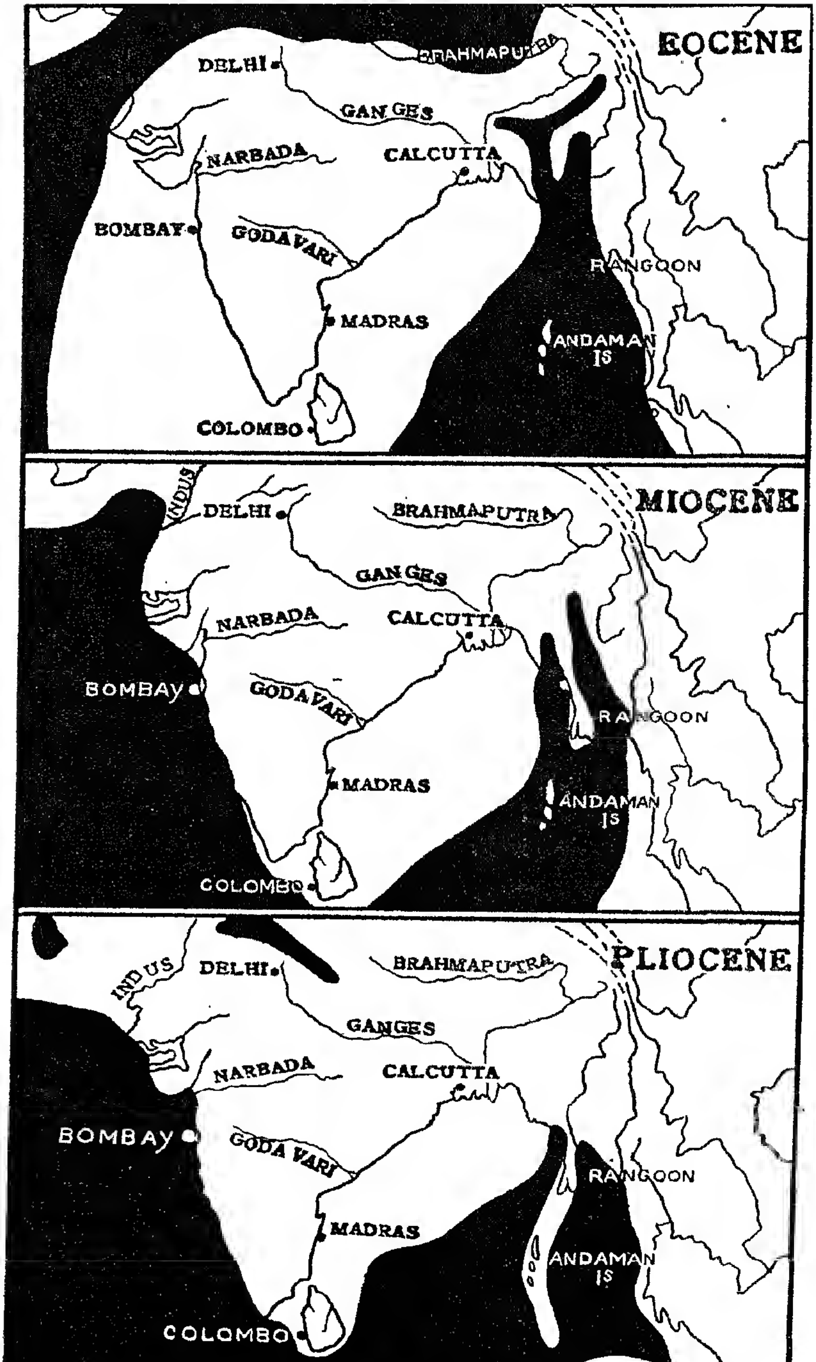
1. Certain species are still in the process of evolution and as a result of geographical isolation have developed certain racial features characteristic of well defined geographical areas. There are various gradations in the process of species formation.
2. Through long isolation or some form of habitudinal segregation, endemic species have established themselves in certain characteristic geographical areas.
3. There is definite evidence of the 'Malayan' element in the fauna of India, particularly of Peninsular India.
4. There is definite evidence of a once continuous Indus, Ganges and Brahmaputra river.
5. There is definite evidence of a connection of the Ganges System with the River Systems of the Mahanadi and Godavari.
6. There is evidence that certain desert-loving forms migrated into India from the north-west and spread over the Peninsula and Ceylon.
7. There is some evidence that Chota Nagpur plateau formed a link in the route of migration of 'Malayan' forms to Peninsular India.

An attempt will be made later to elucidate all these points by referring to the evolution of the present-day physical features of India.

Distribution of the Species of Indo-Chinese Subregion.

Of the 34 species recorded from this subregion, as many as 9 (Nos. 14, 15, 20, 29, 31, 41, 44, 55 and 58 of the list) are endemic in the Trans-Himalayan Mountainous Area, one is endemic in Annam (No. 12 of the list) and one in the Eastern Himalayas (No. 38 of the list). Eight species (Nos. 3, 13, 18, 24, 25, 26, 28, 33 and 59) are common to the Great Plains of Indo-China, Tenasserim and Peninsular Siam. Four species (Nos. 9, 23, 51 and 53) are found in the Trans-Himalayan Mountainous Area, the Great Plains of Indo-China, Tenasserim and Peninsular Siam. Four species (Nos. 16, 30, 32 and 61) are common to the Trans-Himalayan Mountainous Area and Annam. One species (No. 11) is found all over the Indo-Chinese Subregion; one (No. 10) is found in the Eastern Himalayan Area, Trans-Himalayan Mountainous Area and the Great Plains of Indo-China; one species

DISTRIBUTION OF LAND & SEA IN INDIA
DURING EOCENE, MIOCENE & PLIOCENE PERIODS

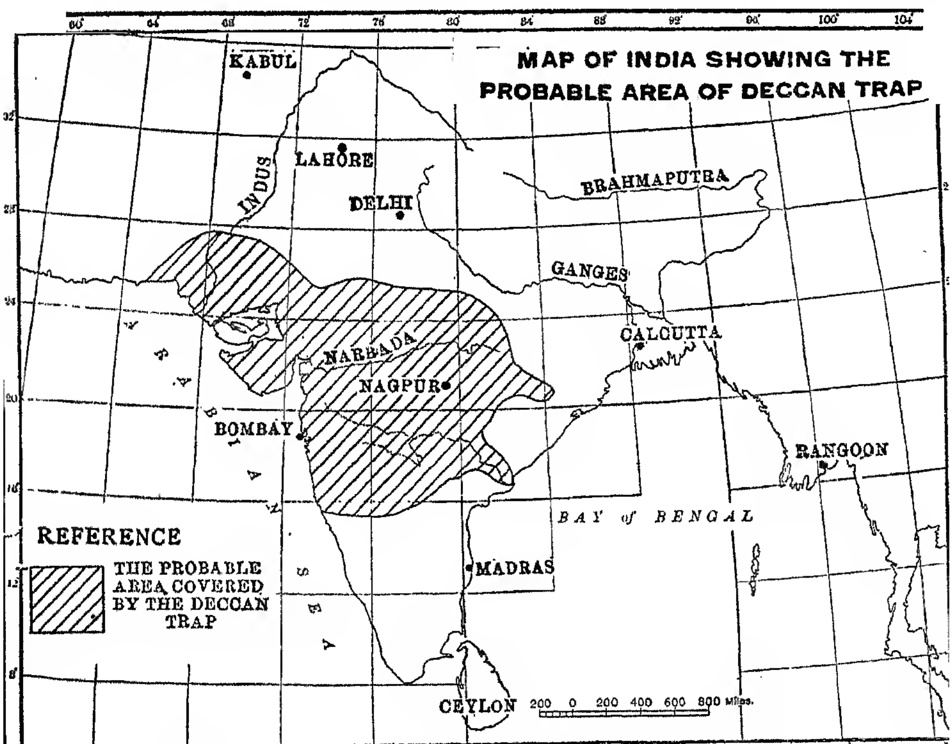


Text-fig. 3. of India showing the distribution of land and sea during the Eocei Miocene and Pliocene periods.
The reproduced here are parts of maps photographed from some work of which the reference is lost.

(No. 33) is found in Trans-Himalayan Area and Tenasserim; one species (No. 17) is found in the Trans-Himalayan Mountainous Area, Annam, Peninsular Siam and Tenasserim; one species (No. 48) to the above three regions as in No. 17 and also the Great Plains of Indo-China; one species (No. 60) is found in the Trans-Himalayan Mountainous Area, Annam, and Great Plains of Indo-China and one species (No. 47) to all the areas except Annam. It will be noticed that the largest number of species is found in the Trans-Himalayan Mountainous Area and particularly in Southern China.

Probable Centre of Origin of the Fauna.

From the distributional records noted above, it would seem probable that Southern China formed the original home of these animals whence they radiated towards the south-west into Burma and India; into Burma, Siam and the Malay Peninsula and Archipelago and south-east to Indo-China and Annam. The directions of the mountain ranges and the rivers in the Indo-Chinese Subregion support this view and I shall show later that geological evidence also favours such a hypothesis.



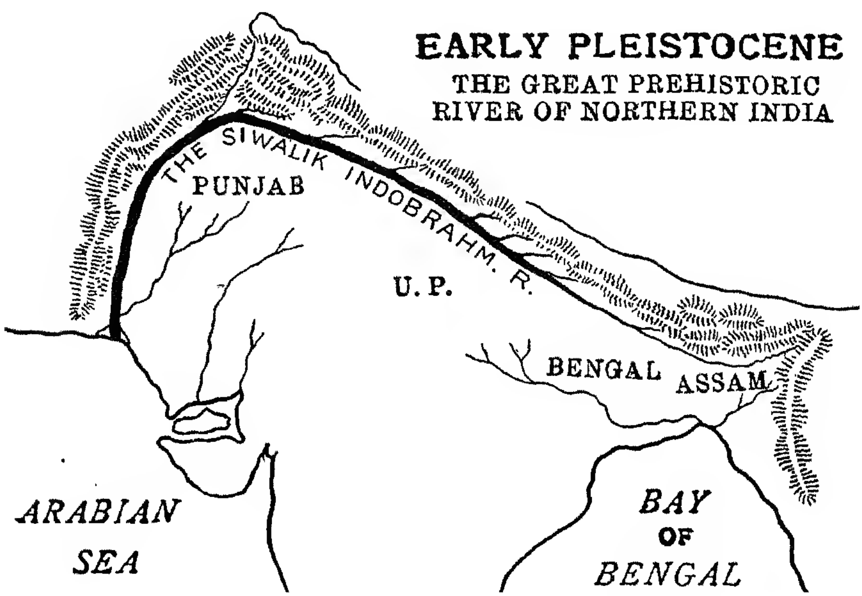
Text-fig. 4. Map of India showing the probable area covered by a succession of lava flows constituting the Deccan Trap.

Evolution of the Geography of South-eastern Asia.

During the Gondwana period, when Australia, South-eastern Asia, East Africa and South America were parts of a single continent, Gondwanaland, the earth underwent a slow gentle buckling of the earth's crust which produced a series of extensive east-and-west valleys. During such a period crocodiles must have extended all

over Gondwanaland and this would explain their present-day discontinuous distribution.

At the end of the Gondwana period, in late Cretaceous or early Tertiary, there was an intense folding of the crust accompanied by the upheaval of the Alpine-Himalayan System, which dismembered the Gondwana Continent and gave the Indian Peninsula more or less its present outline and caused the eruption of lava which formed the Deccan Trap. The Himalayan upheaval, in its initial stage, probably confirmed some of the Gondwanaland valleys, but later the movements became more violent on lines tending north and south and disorganised the older drainage system, for with the upraised Central Asia as a vast block with long slopes towards the east and south the general drainage from Tibet was fundamentally altered. The west-to-east courses of the Upper Brahmaputra, the Hwang Ho, the Yangtze Kiang and the Si Kiang are probably the modern survivals of the ancient east-to-west rivers, but later arose the north-to-south rivers, such as the Dihang, the Irrawaddy, the Salween and the Mekong. The latest east-to-west big river was the Indobrahm or the Siwalik River along the southern base of the



TEXT-FIG. 5. The Indobrahm or the Great Prehistoric River of Northern India. *After Dr. D. N. Wadia.* (*Proc. Nat. Inst. Sci. Ind.* 4, 389, 1938.)

The Indobrahm was the successor of the Nummulitic Gulf which stretched from the head of the Sind Gulf to the Punjab and thence along the foot of the ombryonic Himalayan chain through Simla and Naini Tal to Assam. It carried the combined discharge of the Brahmaputra, the Ganges and the Indus rivers and seems to have existed all through the late Tertiary and early Pleistocene times.

Himalayas in the Pleistocene period. We have ample evidence of the existence of such a river in the distribution of the crocodiles and chelonians referred to above. It must be noted that there was no present-day lower Ganges at that period and, therefore, probably there was no gap between the Garo Hills in the east and the Rajmahal Hills in the west.

The Himalayan uplift was in several major and minor stages and from the violent earthquakes witnessed in this region, it is evident that they are still very unstable and are still rising. Usually three major stages are recognised. During the first

stage the central axis of the Himalayas was upheaved. The second stage about Mid-Miocene upheaved the central part of the range and the third phase came at the end of the Tertiary period when the sub-Himalayan zone was added to it. The last phase is still continuing and was responsible for the uplift of the Siwalik Hills and the disturbance of the Karewas in Kashmir.

The orogenic movements from the north that produced the Himalayas, met with strong resistance from the very old block of the Indian Peninsula, the middle portion of which, however, sagged and in course of time gave rise to the alluvial plain of the Ganges and a concave outline to the central part of the Himalayas. The effect of the subsidence of the northern part of the Peninsula also affected the Vindhyas and the Satpuras which were at one time much loftier mountains and formed continuous ranges extending between the Assam Himalayas on the one hand and the Gujarat Western Ghats on the other. The Himalayan movements met resistance in the east by the horn of the Peninsula presented by the hills of Assam and in the west by the hills round about Kohat. At both these points the Himalayas were bent round and took a more or less north-to-south direction. The direction and intensity of these movements determined the evolution of the zoogeographical features of India and in consequence the migration or dispersal of the animal life.

Simultaneously with the rise of the Himalayas, lava flowed out from fissures in several parts of the Indian Peninsula and gave rise to the Deccan Traps (*vide supra*, text-fig. 4). Like the Himalayan movements and probably contemporaneous with them, the outbursts of lava also occurred at varying intervals and during the quiescent period animals from neighbouring areas migrated to these lava rocks and some remains of them became entombed in the infra- and inter-trappean beds. The last lava outburst may be contemporaneous with the formation of the Siwalik hills in the Pleistocene period or may be even younger than that as is evident from the distribution of the present-day forms. The lava flows completely annihilated the then existing fauna and recolonisation occurred during the dormant periods.

In the Trans-Himalayan Area, particularly in Yunnan, there were corresponding earth movements. To explain the origin of deep canyons of the rivers of Yunnan and Western China, it is believed by some that there was a regional uplift of some 6,000 to 10,000 feet in very recent geological times. Gregory and Gregory (1923) have, however, found no evidence of any post-Pliocene high regional uplift of this area. According to them, the physiography of central and south-western China could be explained by the subsidence of the surrounding country, which produced long slopes downward to the east and the south. The geographical distribution of animals supports the latter view.

One more palaeogeographical fact must also be borne in mind in connection with the origin and evolution of the Indian fauna. In his study of the evolution of the river system of south-eastern Asia, Gregory (1925) found that in the Trans-Himalayan Area the rivers on the west generally beheaded the rivers on the east and thus diverted their waters, and consequently the aquatic fauna, westwards. Probably this happened several times contemporaneous with the phases of the Himalayan uplift and enabled the fauna to spread westwards in a series of waves. Evidence of such waves of migration is clear even among the Chelonians referred to above.

Age of the Present-day Crocodiles and Chelonians.

Though the Crocodiles made their first appearance in the Upper Cretaceous of Europe and North America, the fossil forms of Gharials (*Gavialis*) are known from the Pliocene deposits of the Siwalik Hills and the Narbada Valley. The Chelonians are a much older group, for they are found in the Triassic much as we see them now. Their greatest development was towards the end of the Mesozoic and in the early Tertiary Period. As shown above, some of the present-day Indian forms are known from the fossils of the Siwalik Hills and are, therefore, at least as old as the Pliocene.

THE ORIGIN AND DISPERSAL OF THE FAUNA.

As in the case of freshwater fishes, the distributional records of Indian Crocodiles and Chelonians show that they originated on the Yunnan tableland when the conditions were probably somewhat warmer than they are at present. With the subsidence of the surrounding country, probably in a series of five or six phases, and the production of long slopes downward to the east and the south, the fauna became dispersed along these two routes in the first instance; the eastern branch colonised French Indo-China and Annam, while the southern branch became dispersed into the hills of Burma, Siam and the Malay Peninsula. The northern portion of this branch, through a series of river captures, was deflected westwards to the Eastern Himalayas and the Hills of Assam. There is a barrier, yet undefined, in Central Nepal, which prevented the westward migration of the fauna along the Himalayas, but the Assam Hills were then continuous with the Rajmahal Hills and there stretched across India loftier ranges of the Vindhya and Satpura Mountains which captured the monsoons and produced ecological conditions similar to those of the Eastern Himalayas, Assam Hills and the Western Ghats. In certain parts of the Chota Nagpur plateau similar conditions prevail even up to the present day. Along this range the fauna was dispersed to the Western Ghats and thence along them to the south and Ceylon. This was the first wave and could explain the occurrence of Malayan or Indo-Chinese element in the fauna of Ceylon. The second wave came with a very rich new faunal element after Ceylon had been separated from the mainland through subsidence. This would explain the number of characteristic species in the Malabar Tract (Cochin, Travancore) south of the Palghat Gap. Through further subsidence or faulting the Palghat Gap made its appearance and prevented the third wave from reaching the extreme south of the Peninsula. Through the latest eruption of the lava, a considerable north-western portion of the Deccan became denuded of animal life and when normal conditions returned, a fourth wave repopulated it. There were then shorter waves which did not reach the Western Ghats but spread for varying distances along the Satpura and Vindhya Trend of Mountains. It was at this stage, that the Indobrahm river of the Siwalik period became dismembered, the Garo-Rajmahal Gap formed, the present-day Ganges came into existence and flowed through the Garo-Rajmahal Gap to the Bay of Bengal. Further changes in the migration of the mountainous forms between the Garo Hills and the Rajmahal Hills became interrupted but the Eastern Himalaya and the Assam Hills continued to receive eastern elements.

The Western Ghats had another contact with the Himalayas through the Arravali Range and some Western Himalayan forms spread over this range southwards. Similarly, the high country beyond Delhi to the Baluchistan and West Punjab Hills, which must have been more pronounced once, served to deflect some of the north-western forms to the south. However, this element is represented only by a few forms.

The most remarkable thing to note is that all these changes had occurred during the Pleistocene or later periods when the present-day fauna had established itself.

CONCLUSIONS.

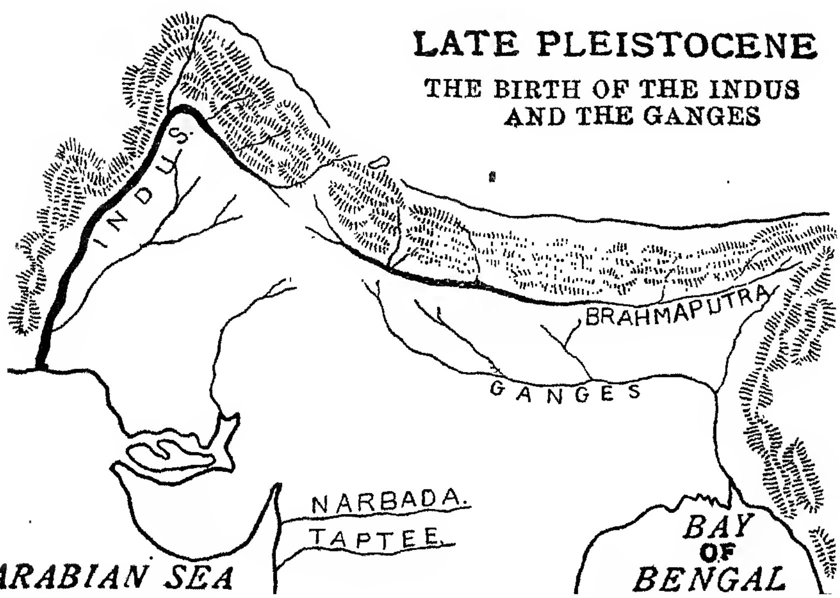
In his chapter on Zoogeography, Smith (1931, p. 15) remarked:

> 'The dispersal of most of the species that exist today took place at a time when the geographical configuration of the country was very different from what it is today. The number of species that are common to the islands of the Malay Archipelago and the continent of Asia is one proof of this; the present distribution of Gharial (*Gavialis gangeticus*) and of the Freshwater Turtles, e.g., *Chitra* and *Pelochelys*, in river-systems that are not now connected together is another. It seems equally certain that the Indo-Chinese hill tortoises, *Testudo elongata* and *Geoemyda tricarinata* did not extend their range into the peninsula of India (Chota Nagpur) by crossing the Gangetic Plain. True hill species for this reason are of greater interest and value in the study of zoological distribu-

tion than lowland forms. They are just as much isolated by the conditions under which they live as if they inhabited islands, and their occurrence on widely separated mountain ranges is good evidence that a more direct connection between these ranges existed in past times than is to be found today.'

All this is very true, but Smith failed to indicate the connections which could account for the many anomalies in the distribution of the Crocodiles and Chelonians. In fact, in his second volume in the *Fauna* (1935, p. 15) on Sauria (Lizards), he is unable to explain these anomalies of distribution. He states:

'The close affinity which certain Indo-Chinese and Malayan lizards have with others that inhabit Southern India—the northern part of the Indian Peninsula being without them—raises an interesting point in zoological distribution. The resemblance which *Dasia olivacea* bears to *D. subcaeruleum*, *Lygosoma maculatum* to *L. dussumieri*, and *Riopa bowringi* to *R. albopunctatus*, is so close that one feels convinced that if one has not been derived from the other they must surely have had a common ancestor. The genus *Draco* has a similar distribution; *Varanus salvator* occurs in Ceylon and in Indo-China, but is absent from the whole of the Indian Peninsula; and there are similar parallels in distribution among the mammals, birds, fishes, and insects. Why are they absent from Northern India? Have they died out in that area, or was there at one time a more southern route across the Indian Ocean by which they could travel?'



TEXT-FIG. 6. Dismemberment of the Indobrahm in the late Pleistocene Period and the birth of the Indus and the Ganges as separate rivers. *After Dr. D. N. Wadia.* (*Proc. Nat. Inst. Sci. India*, 4, 389, 1938.)

'At the end of the Siwalik epoch an uplift of the ground between Hardwar and Bikaner disconnected the Indus system from the Ganges portion of the Indobrahm, thus splitting up that river into two separate drainage basins' (Wadia).

I believe the route I have suggested above along the Vindhya-Satpura Trend of Mountains meets with all the requirements of zoogeography in India so far as the occurrence of Malayan element in its fauna is concerned. The most interesting point is that all these changes were, comparatively speaking, recent and that they are more or less supported by the evidence that has accumulated in recent years concerning the palaeophysiography of south-eastern Asia. For instance, Wadia (1943, p. 41) has pointed out that

'The period immediately succeeding the Tertiary was a period of intense orogenic activity in North-West India, it being the final phase of the uplift of the Himalayas,

during which, to judge from various evidences observed in the Pir Panjal, the Kashmir Himalayas were lifted from 5,000 to 8,000 feet. Tho tilting and folding of the river and lake-formed Karewas with the fossil plants, fish, batrachians, olephas, rhinocoros, and a few human implemonts, and their extension to altitudes up to 11,500 foet, afford a rough estimate of the extent of the movements and of their time duration.'

These intense movements in the North-West India must have had percussions over the entire Indo-Gangetic Basin and affected the Vindhya-Satpura trend of mountains. It seems likely that orogenic movements of this period may have dismembered the Indobrahm river and produced the Garo-Rajmahal Gap which blocked the further migration of the so-called Malayan fauna to South India.

Acknowledgments.

I am grateful to Dr. Malcolm A. Smith, Lt.-Col. R. B. S. Sewell, Dr. A. T. Hopwood and Professor H. L. Chhibber for kindly going through the typescript and favouring me with their comments and suggestions. Dr. Hopwood's note is reproduced here in its entirety under 'Discussion'.

Summary.

The distribution of Crecodiles and Chelonians in Ceylon, India, Burma and Farther East is tabulated in accordance with the data given in Smith's revised edition in the *Fauna of British India* series. Short descriptions of the zoogeographical areas recognised by Smith and of the ecological factors influencing animal life therein are given.

Of the 61 species of Crocodiles and Chelonians inhabiting the Indian Region, one species of croeodiles and four species of turtles are either estuarine or marine. Of the remaining 56 species, 8 are common to the Indian and Indo-Chineso Subregions, 14 are confinod to the Indian Subregion and 34 to the Indo-Chinese Subregion. The significance and value of distribution of species of each of these groups is separately elucidated.

The distribution of species of the Indian Subregion shows: (i) that somo of the species are still in the process of evolution and that in certain characteristic ecological complexes a number of endemic species have evolved, (ii) that there is definite evidence of the migration of Malayan forms to Peninsular India, (iii) that the Indus and the Ganges must have formed a continuous river system once and that at some stage tho Mahanadi and Godavari had connections with the Ganges System, (iv) that thero is evidence of the migration of certain North-Western desert forms to Peninsular India and Ceylon, and (v) that tho Chota Nagpur plateau must have beon in the route of migration of the Malayan forms to Peninsular India.

Southern China seems to be the probable centre of origin of the fauna and roference is made to the antiquity of the Croeodiles and Chelonians. It is shown that tho present-day Indian forms are at least as old as the Pliocene.

A brief account of the evolutien of the geography of South-East Asia is given and tho origin and dispersal of the fauna is discussed. The most remarkablo thing to note is that the various palaeogeographical changes responsible for the present-day distributien of animals in India seom to be of comparatively recent origin and are probably associated with tho intense orogenic activity immediately after the Tertiary when tho Kashmir Himalayas were lifted from 5,000 to 8,000 feet.

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Discussion.

Dr. A. Tindell Hopwood of the British Museum (Natural History) sent the following comments with regard to the evolution of the geography of South-Eastern Asia and distribution of certain selected species.

'The E.-W. valleys of Central Asia are connected with the Hercynian (i.e. Carboniferous) orogenesis. Their relatively simple arrangement was strongly influenced by the much later Alpine-Himalayan movements which began at the very end of the Cretaceous, continued at intervals during the Tertiary, gave a last heave at the beginning of the upper Pleistocene and have not yet entirely died away.

The curious disposition of the mountains to the W.-N. and E. of India is a result of the squeezing out of the Tethyan geosyncline between Laurasia advancing from the north and the Indian block, or fragment of Gondwanaland from the south. The opposing fronts squeezed the soft contents of the geosyncline into the E.-W. Himalaya but, since the Indian block was much narrower than Laurasia its advance threw the sediments on either side into N.-S. folds as in E. Baluchistan and in Burma.

Eventually Laurasia over-rode the Indian block, or if you prefer it, India dived under Laurasia. In any event the elevation of the Tibetan plateau was caused by this movement which also tilted the Indian block and carried down the Vindhya-Satpura hills. In the fore-deep so formed on the southern front of the Himalaya the Indo-Gangetic plain was formed from the sediments washed down from the rising mountains.

The Vindhya-Satpura ranges, the Eastern Ghats and the Nilghiris are extremely ancient features representing early Palaeozoic (Cambrian ?) orogenesis.

If the Brahmaputra is an old river which originally flowed in an E.-W. valley, its mouth must have been somewhere on the China Sea, and one is tempted to speculate that its eastward continuation is now represented by the Yangtse Kiang. If that were so the interruption would have been brought about by the elevation of the mountains which now fill the gap between the two rivers and the Brahmaputra would be a very old river indeed dating back to Permian or even Carboniferous times. It seems more likely, however, that the river did not exist prior to the first elevation of the Himalaya and that it took its origin from the drainage of the northern slope of that chain accumulating in a parallel valley. There it flowed eastward. The southward bend in Tibet is conditioned by the general structure of that area, and the same factor governs the westward bend in northern Assam.

The reversal of drainage which ended the Indo-Brahm and gave rise to the Ganges and Indus is post-Middle Pleistocene date. The same earth-movements were responsible for the formation of the Garo-Rajmahal gap.

Remarks on the Distribution of certain selected Species

a. *Gavialis gangeticus*	Occurs in regions 1, 3, 9.
b. *Crocodilus palustris*	1, 2, 3, 4, 5, 6, 7, 8.
c. *Cyclemys mouhoti*	8, 9, 11.
d. *Geoemyda tricarinata*	7, 8.
e. *G. trijuga*	5, 6, 7, 8, 9.
f. *Kachuga dhongoka*	3, 8.
g. *Batagur baska*	3, 9, 12.
h. *Testudo elongata*	7, 8, 9, 10, 12.
i. *Lissemys punctata*	1, 3, 4, 5, 6, 9.
j. *Chitra indica*	1, 2, 3, 8, 9, 11, 12.

Of these *b*, *i*, *j* are old species in India and invaders in Indo-China, *c* and *h* are old in Indo-China and invaders in India. The difficult genera are *Geoemyda*, *Kachuga*, and *Batagur*. *Geoemyda* probably invaded India and *Kachuga* invaded Indo-China. *Batagur* might have done either, but I think it went from West to East.'

The following discussion took place when the paper was communicated by Dr. Hora at the Ordinary General Meeting held on May 4, 1948 :—

In communicating his paper entitled 'The distribution of Crocodiles and Chelonians in Ceylon, India, Burma and Farther East', Dr. S. L. Hora gererally referred to the distribution of the Vertebrata in India, with particular reference to the so-called Malayan affinities of the

vertebrate fauna of the Malabar Tract of the Western Ghats. He invited attention to the fact that after the completion of the *Fauna of British India* volumes on Vertebrata, Blanford published an account of the distribution of vertebrate animals in the *Philosophical Transactions of the Royal Society of London* in 1901. Some of these *Fauna* volumes have now been revised and in the light of new knowledge concerning the systematics and geographical distribution of the various animals, it was now possible to comprehend more fully the zoogeography of the forms showing discontinuous distribution. This article, Dr. Hora pointed out was the first of a series that would be published on this subject.

Dr. Hora then described the probable routes of migrations of the Malayan forms to the Western Ghats and stated that as Bay of Bengal is a very old feature of the physiography of India, the migration of freshwater turtles and tortoises could not be across this region. As most of these forms were not found in the Western Himalayas, they could not have been pushed down as a result of glaciation. The resemblance of the Chelonian fauna of the Chota Nagpur Plateau with that of Assam, Burma and Farther East on the one hand and with that of the Malabar Tract on the other showed that Chota Nagpur must have formed a part of the route of this migration. This, Dr. Hora said, confirmed his earlier views based on the study of distribution of torrential fishes, and he was feeling more and more convinced that the Satpura-Vindhya trend of mountains must have been continuous once with the Assam Hills and the Eastern Himalayas on the one hand and with the Gujerat section of the Western Ghats on the other.

Dr. Hora then referred to the necessary climatic conditions over the Vindhya-Satpura trend for making possible the migration of the rain-forest dwelling species common to the Malabar Tract and Assam-Burma region. He opined that when this migration took place the Satpuras and the Vindhyas must have been much higher ranges which could intercept monsoons more effectively so as to give an annual precipitation of 100″ to 150″ per annum on their slopes resulting in luxuriant vegetation. He stated that Dr. S. K. Banerji, Director-General of Observatories, has computed that for this amount of precipitation, the Satpuras must be raised to 6,000 to 8,000 feet above sea-level.

Referring to the geological period when this migration took place, Dr. Hora stated that the evidence so far available to him showed that active migration was facilitated by orogenic movements consequent upon the uplifts of the Himalayas during the later Tertiary or Quarternary Periods.

Dr. S. K. Banerji explained with reference to the monsoon currents in this region how the figure of 6,000 to 8,000 feet elevation of the Satpuras was computed so as to give Dr. Hora climatic conditions, consequent on rainfall, equivalent to those prevailing in Assam and the Malabar Zone. He stated that from the very nature of the proposition put to him, it was difficult to answer with any degree of precision but the values given could be taken as very good approximations.

Dr. S. P. Agharkar stated that the hill-top floras of the Western Ghats and the Assam-Burma Hills showed resemblances almost identical with those described by Dr. Hora among the faunas. He also agreed with Dr. Hora that the Satpura-Vindhya trend of mountains could serve as the route of migration when the climatic conditions over the entire area were more or less uniform and conformed with the present-day conditions in the Eastern Himalayas, Assam Hills and the Malabar Zone.

Dr. D. N. Wadia stated that as a geologist he welcomed the studies that were being conducted by Dr. Hora, but that more detailed information and data were necessary to establish the probable route of migration of the Malayan forms to the Western Ghats.

BULLETIN No. 9

OF

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Our Bulletins

National Geographical Society of India, Benares is in the third year of its existence and this is our ninth Bulletin. When the Society was inaugurated, stimulating messages were received from our revered leaders including Dr. Rajendra Prasad, the Hon'ble Pandit Govind Ballabh Pant, Premier, the United Provinces, His Excellency Dr. Kailash Nath Katju, the Hon'ble Shri Sampurananand, Minister of Education and Finance, the United Provinces, Mr. Sarat Chandra Bose, Pandit Govind Malaviya, Member, Constituent Assembly, Shri Padampat Singhania, Governing Director, J. K. Group of Industries, Shri Ram Ratan Gupta, Banker and Mill Owner, Cawnpore, Seth Shanti Prasad Jain of Messrs Dalmia-Jain Industries and Professor E. G. R. Taylor of the University of London. These messages were published in our Bulletin No. 3. We had similar letters from Mahatma Gandhi, the Hon'ble Pandit Jawaharlal Nehru and Dr. John Mathai. Since the publication of the above messages we have received similar messages of encouragement from Dr. S. S. Bhatnagar, D.Sc., F. R. S., Director, Scientific and Industrial Research, New Delhi, Pandit Hirday Nath Kunzru, Dr. Iqbal Narain Gurtu, ex-Vice Chancellor, Allahabad University, Dr. S. Subramanyam, M. L. A., Karaikudi, Dr. H. J. Bhabha, Ph. D., F. R. S., Tata Institute of Fundamental Research, Bombay, etc.

Likewise we have received stimulating messages of good-will and wishing us all success from foreign geographers, the prominent among those being Dr. L. Dudley Stamp, Professor of Geography in the University of London, Dr. Austin Miller, Professor of Geography in the University of Reading, Professor Frank Debenham of the University of Cambridge, Professor Kenneth Mason of the School of Geography, Oxford.

Among American Geographers we had similar messages from Dr. G. B. Cressey, Chairman, Department of Geography and Geology, Syracuse University, Dr. Shannon McCune, Head of Geography Department, Colgate University, Hamilton,

New York, Professor Clarence F. Jones of Northwestern University, Illinois, Dr. Otis P. Starkey of Indiana University and President, American Society for Professional Geographers, etc.

Professor C. A. Cotton of Victoria University College, Wellington and John A. Bartrum of the University College, Auckland, New Zealand were also good enough to send us similar messages. Among similar correspondents from Australia we are glad to mention the names of Professor Macdonal Holmes of Sydney, Professor E. de C. Clarke and Dr. R. W. Fairbridge of the University of Western Australia. Dr. Alex du Toit, author of "Our Wandering Continents" particularly appreciated our Bulletin No. 5 on "the Origin of Forces responsible for Disrupton of Continents, Mountain Building and Continental Drift, etc."

These messages we hope to print in the coming issues of our Bulletins.

It has been particularly gratifying to us that these Bulletins found a great demand not only in India but abroad also. We had a great number of orders from the United States of America through reputed concerns of booksellers and publishers. Some of the Geographers there have become our regular members and subscribers. Recently Dr. George J. Miller, Editor of the *Journal of Geography* wrote: "It appears to me that these Bulletins should be of real interest to many geography teachers in this country and we hope that you will hear from a number of schools and libraries".

A numbr of foreign Geographical Societies like the *Societie de Geographie, Paris, Institute Geografico Militare, Firenze,* Italy, Canada Department of Mines and Resources, University of Illinois Library, *Ceylon Geographical Society,* etc. have established their exchange relations with us. We shall be glad to establish similar exchange relations with other similar societies as well.

We have been constantly thinking of converting our Bulletins into a *Quarterly Magazine of National Geographical Society of India, Benares.* For this we request geographers, both in India and abroad, to send us their valuable contributions on Indian

geography. We do hope they will help us in advancing geographical knowledge in general and that of India in particular for which we stand.

In this connection one of our difficulties may also be mentioned. There exists a Paper Control Order in India. We have approached the District Supply Officer, Benares and the Paper Controller, Allahabad, but without much success. In view of the importance of our Bulletins, which so many revered leaders of India and foreign geographers have appreciated and emphasized, we wonder, why our request has not met with a suitable response, especially in view of the fact that in a whole year we use only a few reams of paper. We have been advised to approach The Food Commissioner, Civil Supplies, B Department, Secretariat, Lucknow and it is strongly hoped that in view of our such a trifling demand our request will be complied with without further delay. This request is being made especially for whatever contribution we can make towards the scientific development and advancement of the country. We have positively no axe to grind. In view of the fact that large quantities of paper are being used in printing trash, we again strongly hope that we will be permitted to use suitable type of paper. In the meantime our Bulletins appear on uncontrolled inferior type of newsprint. Our motto is to serve and advance geographical knowledge.

Acknowledgements

The cost of printing this Bulletin has been met out of a grant made by the National Institute of Sciences of India, Delhi. We express our sincere thanks to the Council of the Institute for this grant.

Fundamental Conceptions of Zoogeography[1]

BY

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Contents

Introduction

Last year when I came to address the members of the National Geographical Society of India (Hora, 1947), I was asked "What is the connection between Zoology and Geography ?" I must confess that I was greatly surprised at the question, for I felt that in a University, where both Zoology and Geography are taught up to the M.Sc. and higher standards, some general knowledge of animal geography must be a commonplace thing. Since then, I have learnt that the study of animal geography as a separate subject is not pursued in any university of India and that even its fundamental conceptions are little understood. It is a great pity indeed

1. Text of a lecture delivered to the *National Geographical Society of India, Banaras,* on Thursday, the 29th July, 1948.

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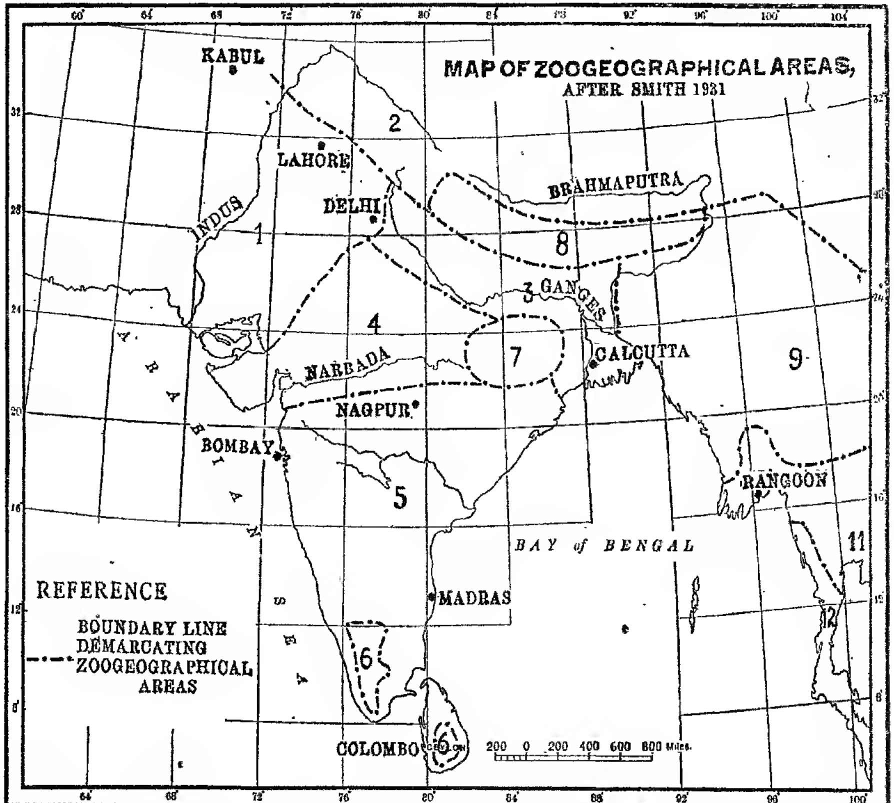

Fig. 1. Map of the Zoogeographical Areas of India, Ceylon and Farther East as recognised by Dr. M. A. Smith in the revised edition of the *Fauna of British India* on Reptilia. (Reproduced from the block loaned by the National Institute of Sciences of India).

that in the latest edition of Parker and Haswell's *Text-Book of Zoology*, the chapter on Zoogeography has been omitted. In choosing a subject for this evening's talk, I have, therefore, been guided by the above considerations.

The scope of geography has been defined as the study of earth in relation to man and thus it includes everything produced by Nature or performed by Man. Within such wide limits, the study of animals and plants has just as much to contribute to the knowledge of geography as, for instance, geology, meteorology, agriculture, animal husbandry, etc., etc. Without any further apologies, therefore, I shall now take up the consideration of the fundamental conceptions of Zoogeography one by one and show you how the study of Zoology can contribute a great deal towards the understanding of some of the most intricate geographical problems of India.

Topography and its bearing on Animal Distribution

All of you are no doubt familiar with what the late Sir Archibald Geikie said concerning the basis of physical geography of any country. He observed :

> "Geographers are apt to forget that in order to understand the geography of any region, as it now is, we must learn how it has been gradually built up. No country came into existence as it now is. If we would discover how its topography has originated, we must study the results of long-continued geological observation."

The present-day zoogeographical divisions of India, (Plate I) for instance, reflect the changes which the country has undergone in the past, though the stage now reached is nearly completed with regard to large areas. The distribution and biological peculiarities of the living fauna give us abundant material for restoring palaeogeographical conditions, mostly of the late Tertiary or Quaternary periods. I shall illustrate this point by an example. After a long and continued observation on animal distribution,

I (1944) have been led to the view that the gap (Plate II) between the Garo Hills and the Rajmahal Hills is, comparatively speaking, a recent feature of the topography of India.

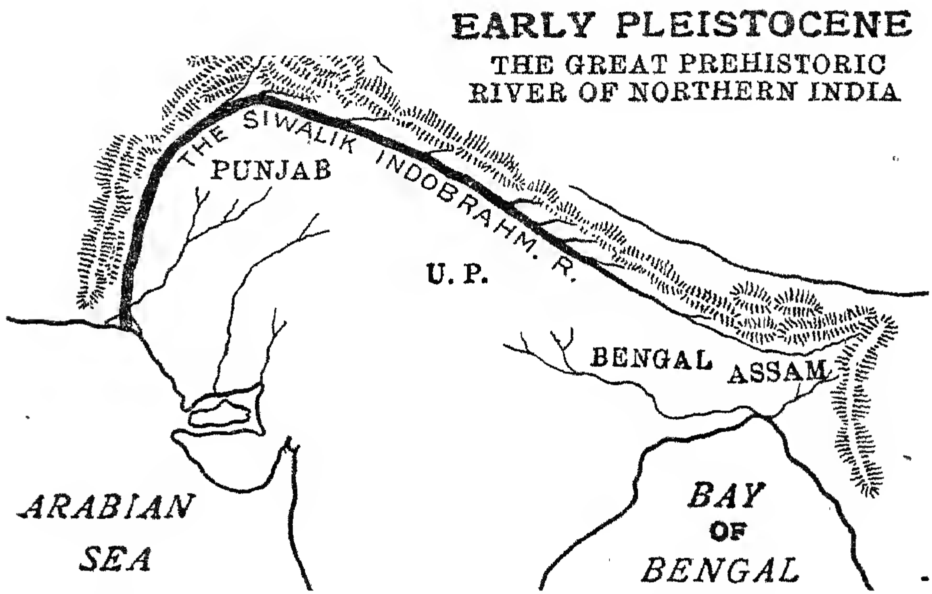

Fig. 1. The Indo-Brahm or the Great Prehistoric River of Northern India. After Dr. D. N. Wadia (*Proc. Nat. Inst. Sci. India*, IV, p. 389, 1938.)

The Indo-Brahm was the successor of the Nummulitic Gulf which stretched from the head of the Sind Gulf to the Punjab and thence along the foot of the embryonic Himalayan chain through Simla and Nainital to Assam. It carried the combined discharge of the Brahmaputra, the Ganges and the Indus rivers and seems to have existed all through the late Tertiary and early Pleistocene times.

The Ganges and the Brahmaputra at present pass through this gap and probably there is a considerable depth of alluvium in this region. However, if you go back to the physiography of India in the early Pleistocene Period, you will find that the Brahmaputra, the Ganges and the Indus together formed a once mighty river, the Indo-Brahm of Pilgrim (1919) or the Siwalik River of Pascoe (1919). I believe, at that period the Garo Hills were continuous with the Rajmahal Hills and thus there existed a continuous range of high mountains between the Assam Himalayas in the east and the northern section of the Western

Plate II

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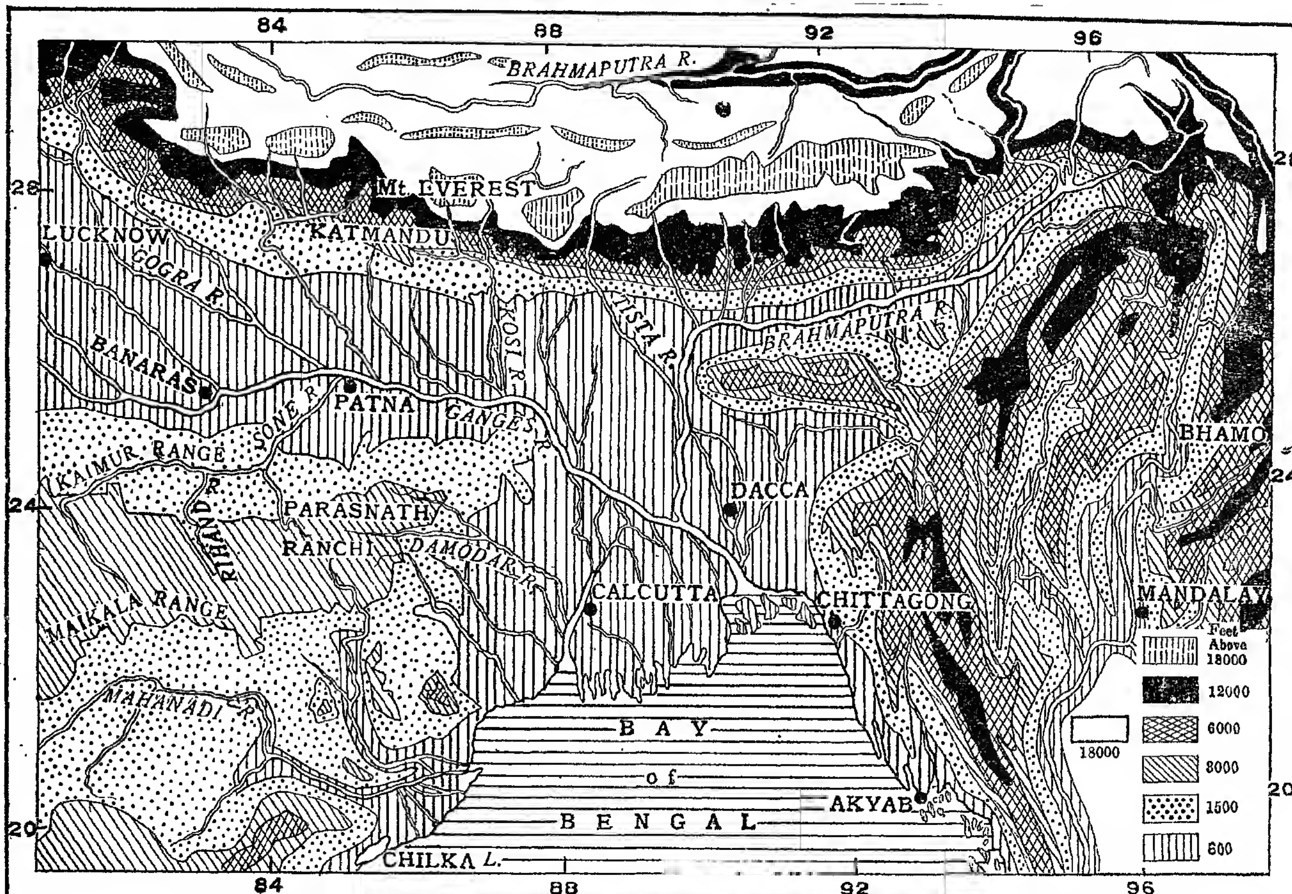

Orographic map of a part of India showing the physical features of the Garo-Rajmahal Gap.

Ghats in the west. The dismemberment of the Indo–Brahm into the Indus, the Ganges and the Brahmaputra occurred in the

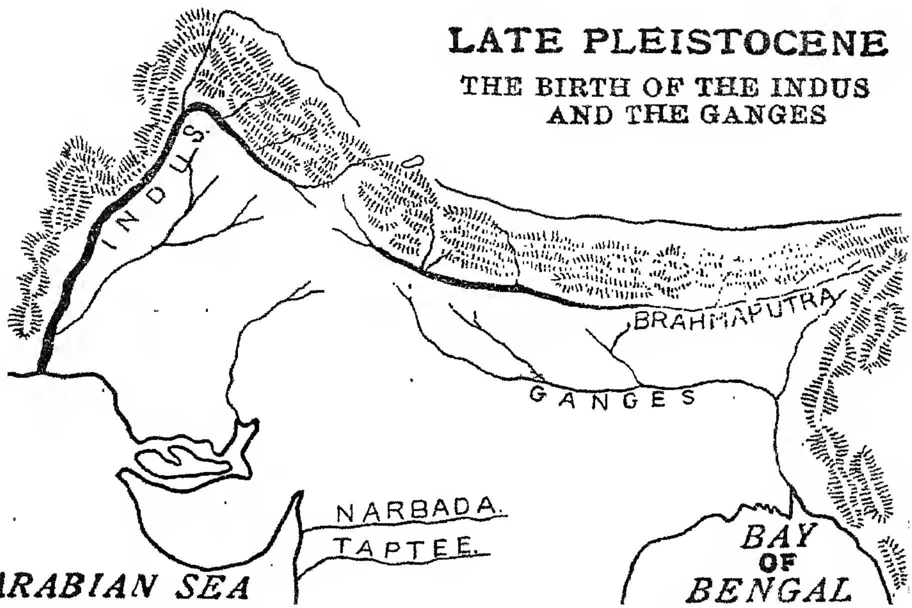

Fig. 2. Dismemberment of the Indo-Brahm in the late Pleistocene Period and birth of the Indus and the Ganges as separate rivers. After D. N. Wadia (*Proc, Nat. Inst. Sci. India.* IV, p. 389, 1938).

'At the end of the Siwalik epoch an uplift of the ground between Hardwar and Bikaner disconnected the Indus system from the Ganges portion of the Indo-Brahm, thus splitting up that river into two separate drainage basins'. (Wadia)

late Pleistocene due to the violent orogenic movements that heaved the Himalayas over 5,000 to 8,000 feet in the Kashmir region (Wadia, 1943). I think the Garo-Rajmahal gap may also have appeared during the same period or even at a later period.

In the above paragraph, I have assumed two topographical features in the physical geography of India in the early Pleistocene Period, namely the continuity of the Indus, the Ganges and the Brahmaputra and the continuity of the Assam Hills and the Vindhya–Satpura ranges of mountains. The geologists, even among themselves, are not yet fully agreed upon both these points, but the zoological evidence is positively in favour of both. The similarity in the aquatic fauna of the three rivers and its

dissimilarity with the fauna of the Peninsular rivers, particularly the Kistna and the rivers to the south of it, are positive proofs of the existence of the Indo-Brahm. Without going into details, reference may be made to the occurrence of the remarkable freshwater porpoise, *Platynista gangetica*, in all the three main rivers of Northern India. The evidence of the distribution of torrential fishes, especially of Malayan affinities, adduced in my talk to you last year is sufficiently conclusive to prove the absence of the Garo-Rajmahal Gap when the so-called 'Malayan Fauna' migrated to the hills of Peninsular India.

Though I have referred above to more recent changes in the topography of India, the earlier physical features of the country are also impressed on the distribution of animals. For instance, the present-day distribution of the Dipnoan Fishes (Australia, Africa and South America) and of the Crocodiles (Northern Australia, Southern Asia, Africa and Tropical America) affords evidence for a once extensive southern continent, the Gondwanaland. Though no Dipnoan fishes are known to occur in India now, their fossil remains found in the Kota-Maleri deposits of the Upper Gondwana Period in the valley of the Godavari River enable us to fill up the gap in their present-day distribution. "*Speaking generally, then, it may be said that discontinuity in the distribution of a species or other group is evidence of its antiquity*". (Italics are mine. Parker and Haswell, 1938, p. 616).

You may rightly enquire at this stage why the Dipnoan fishes are absent from India today and why the highly evolved torrential fishes characteristic of the Assam Hills, Eastern Himalayas and Farther East on the one hand and of the Malabar Zone on the other are absent from the intermediate regions ? To answer these questions, I must first explain the second fundamental conception of Zoogeography.

Ecological Specificity of Faunistic Associations

It is being more and more realised among serious students of biology that any animal or plant has no separate

existence from its environment and, therefore, faunistic zoology must take into consideration problems of animal ecology, which deals with types of environment, adaptation of animals to various environments and "animal sociology and economics". Having studied biological peculiarities of faunistic complexes and the value of their analysis for Zoogeography, Nikolsky (1947, p. 231) has *inter alia* come to the following conclusions :–

1. The main task of the modern Zoogeography consists in analysing the genesis of a fauna's composition, *i.e.*, in elucidating the faunistic complexes which make up a fauna, the history of their origin, their distributional ways and interrelations with other complexes. In fact it is necessary to understand the causes determining the present aspect of a fauna and to establish the regularities to which those alterations are submitted.

2. The unit of a recent zoogeographical investigation should be a faunistic complex or a group of species connected by a common geographical origin, *i. e.*, by development in the same geographical zones to the conditions of which the members of the complex are adapted.

3. The criterion on the ground of which certain species is referable to one or other faunistic complex besides the character of a distribution area is its ecological specificity, *i. e.*, its relation to both abiotic media which are closely connected with each other, being both a sequence of the adaptation to life in a definite geographical zone.

4. In populating a new basin the members of a faunistic complex occupy its part the condition of which approach most the zone where the formation of the complex has proceeded.

Thus in studying animal distribution the knowledge of the topography of the region must be supplemented by a knowledge of the ecology of the animals to be studied. Just as a physical feature can act as a permanent obstacle to the dispersal of the species, an ecological barrier can also be equally effective. For instance, if the ecological conditions are favourable in two regions situated widely apart, the animals of one region can be artificially introduced in the other region and *vice versa*. In the case of India, there are several plants that have been introduced and are now flourishing. Similarly *Gourami* fish introduced from Java into India and *Catla* fish from the northern rivers to the southern waters provide good examples of introduced species.

For the study of Zoogeography, such introduced fauna is of little value. The reverse is also true. The topographical features of the two areas may be similar but if the ecological conditions are different even in two adjoining areas their faunae will be different. The distribution of the Homalopteridae, referred to last year, illustrate these fundamental conceptions of Zoogeography.

The animal associations, as those of plants, are influenced in the main by climatic variations. Temperature, with greater emphasis on mean temperature, is perhaps the most important factor, while moisture conditions are very close to it. Leaving aside the mountains, which have their own climatic peculiarities, soil variation is only secondary to temperature and moisture. In India, it is very striking indeed how strongly the monsoon makes its influence felt over the whole country. Topographical situations, however, make themselves felt through their influence on monsoon winds and thereby on local climate and soil.

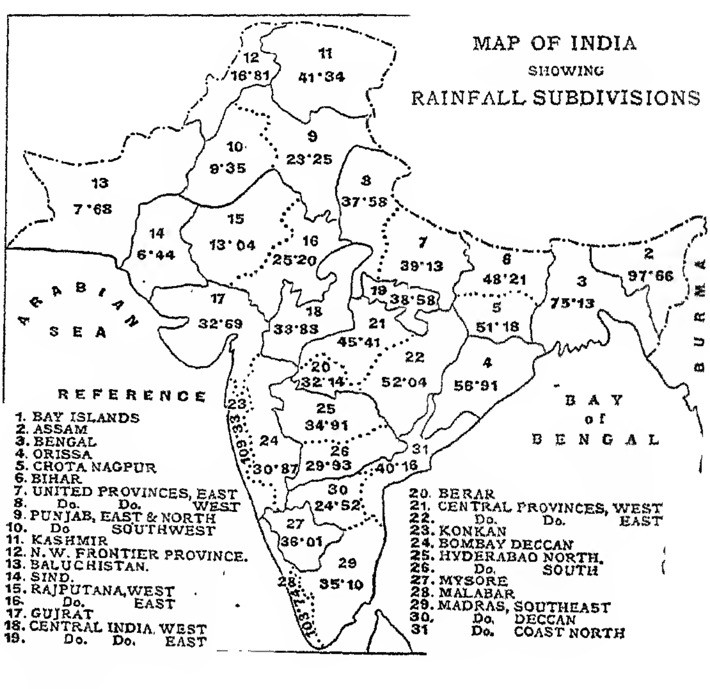

Fig. 8. Map of India showing the rainfall subdivisions. After Dr. L. A. Ramdas (*Empire Journ. Experimental Agric.*, XIV, p. 90, 1946).

Indian geographers are fully familiar that, as regards total annual rainfall, India exhibits an extremely wide range of conditions from virtually rainless tracts in the North-West to nearly 500 inches in Assam. Precipitation over 100 inches is met with in four different parts of the country including Burma, *viz.*, Western Ghats, North Bengal, Assam and Lower Burma. Another characteristic feature of the regions with over 100 inches of rainfall is the seasonal distribution which enables the moisture to be maintained throughout the year, for even a brief period of total desiccation may prove disastrous to the moisture-loving plants and animals. For this reason, though total annual rainfall may constitute an important factor in determining the nature of fauna and flora, its seasonal distribution exerts at least an equally far-reaching influence. Climatic conditions, consequent on rainfall, have therefore,influenced very greatly the present-day distribution of animals in India and it is on climatic conditions that we can explain the discontinuity in the distribution of the Malayan element in the fauna of India.

We are all familiar with the fact that animal life entirely depends on plant life, for even Carnivora which do not eat vegetable matter depend on the flesh of herbivorous animals for their nourishment. The vegetation zones in India (Champion,1936, p.3) have been differentiated on temperature into Tropical (very hot and winterless), Sub-Tropical (hot with a cool winter) Temperate (with a warm summer and pronounced winter) and Arctic (with a short summer and a long severe winter). Ordinarily, latitude and altitude can be equated, but within these four main temperature zones, vegetation can be subdivided on the basis of rainfall. The animal life, mainly depending on vegetation, is also influenced by the same factors as the plants. In considering climates in relation to plants and animals, it is important to bear in mind that "macro-climates" have little significance and that air temperature, humidity, wind velocity, evaporation, etc. , near the ground surface of inside environments of forests, collectively known as "micro-climate", are of special significance (Ramdas,

1946). Unfortunately our knowledge of micro-climates of different parts of India is practically nil and this is indeed a great handicap in the study of animal or plant ecology. I wish, therefore, to emphasize for India what Parr (1945, p. 222) has remarked already regarding Climatology in the United States of America. He stated :-

"It seems obvious to me that what we need is a general meso- and micro-climatotogical survey of our entire country against which the natural sciences, both pure and applied, can compare the results of their own surveys and observations."

For a fuller and more comprehensive knowledge of the plant and animal distribution, some knowledge of meso- and micro-climates of India is absolutely essential.

On the basis of the climatological conception of Zoogeography, the habits and range of distribution of an animal could be ascertained and sometimes the range is continuous and sometimes it is cut up into several *Stations* (Part III). The climatic conditions in different *Stations* may vary slightly and in consequence the animals also vary to a lesser or greater extent at these *Stations* thus giving us a clue to the first step in species formation, *i. e*, isolation and habitudinal segregation as factors in speciation.

Having discussed the roles of topography and climatology in zoogeographical studies, we may now take up the behaviour of animals themselves and thereby discuss the means of dispersal and effectiveness of barriers.

Means of dispersal and effectiveness of barriers

As pointed out by Elton (1927, p. 146), most animal dispersal is directed towards the ordinary feeding, breeding and other requirements of animals but not directly for the spreading of the species. He has done a great service by defining very clearly the terms used in discussing the subject of dispersal. The distribution of the species, a static phase, at any one time is the sum total of three phases—dispersal, establishment of the individual and establishment of the species. The three phases are of a

Plate III

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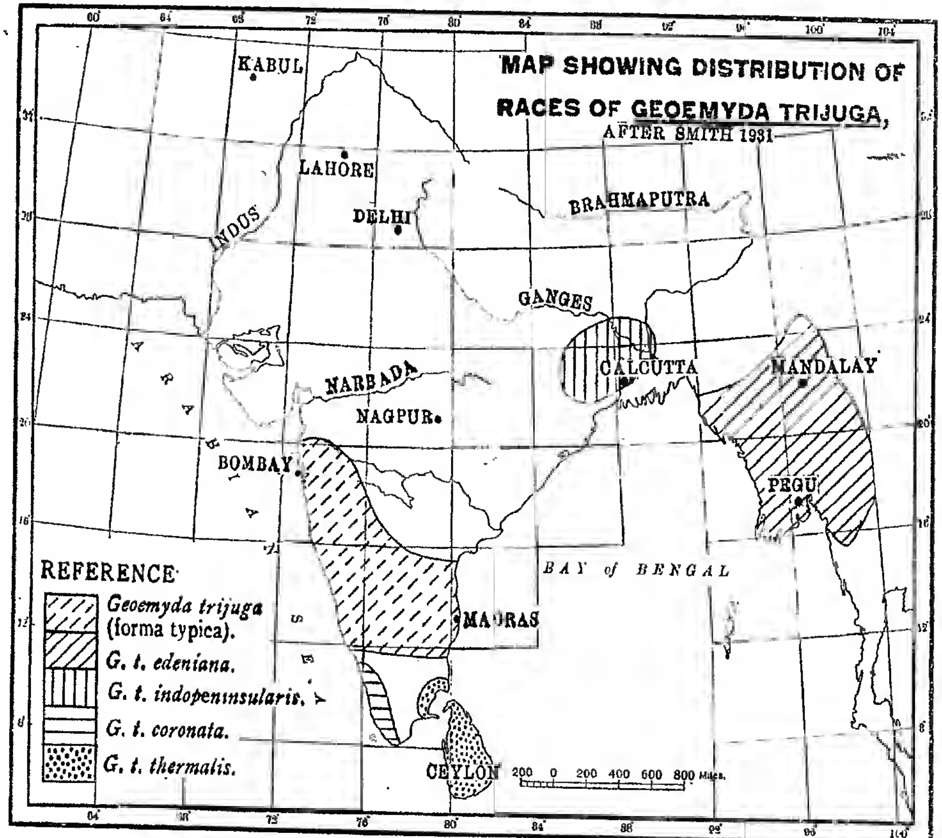

Map of India and Burma showing the geographical raciation and present-day discontinuous distribution of *Geoemyda trijuga* (Schwel). After Dr. M. A. Smith.

dynamic nature and constitute "spread" of the species. As indicated above, ecological succession plays a large part in the slow dispersal of animals. Sometimes, however, there is a definite large-scale phenomenon, such as swarms of locusts, resulting in the spread of the species. According to Elton, much abortive colonisation is always taking place, partly owing to ordinary ecological factors being unsuitable and partly to the difficulty of finding a mate upon arrival at a new place. Three methods of finding the right habitats are employed by animals: broadcasting huge numbers so that a few by chance reach the right habitat; directive migration by means of special instincts or tropisms; and a combination of general broadcasting and local direction-finding.

A barrier in zoogeography implies any permanent obstacle to the dispersal of the species and, as indicated in my last year's talk with reference to the distribution of torrential fishes and torrent-inhabiting birds, the barriers are of unequal importance according to particular animals under discussion. "In close dependence on the means of dispersal we have the fact that the various groups of animals are of very unequal value in the study of distribution. The greater the facilities for the transport of any species across a given barrier the less significance will attach to its occurrence on both sides of the barrier. Conversely, when a species, having few or no facilities for dispersal, is found on opposite sides of an important barrier, the natural conclusion is either that the two areas separated by it were once, so to speak, in zoological continuity, or that the species in question is a very ancient one, and was widely dispersed at a time when the arrangement of the land-surface was very different from what it is at the present day." (Parker & Haswell, p. 615). It will thus be clear that terrestrial and freshwater animals are of more importance, from the point of view of Zoogeography, than marine forms. From among the terrestrial forms, the specialised, moisture-loving animals of evergreen, thick forests and from among freshwater forms the torrential fauna are of still greater importance in zoogeographical studies.

Having dealt with the fundamental conceptions of Zoogeography, it now remains to illustrate the various points discussed above by giving an example from the Indian fauna. Last year, I discussed "Torrential Fishes and the significance of their distribution in Zoo-Geographical Studies" and on the basis of the evidence then adduced put a series of five questions to geologists and geographers of India. Since then I have collected more information regarding the validity of my Satpura hypothesis and I take the liberty to place a few further facts before you.

The Satpura Hypothesis

For a long time, naturalists have recognised the great similarity between the fauna and flora of the Malabar Tract of Peninsular India on the one hand and the Assam Hills, Eastern Himalayas, Burma and Farther East on the other and attempts have been made from time to time to account for this similarity on zoogeographical basis. Medlicott and Blanford (1879, p. lxx) attributed it to the refrigeration of climate during the Pleistocene Ice Age and stated :

"The former extension of the Himalayan glaciers has been shown to have been considerable ; and the occurrence of the Himalayan plants and animals on the higher ranges of Southern India may be due to the retreat of these species in the first place towards the equator, and subsequently, as the temperature increased, to the higher parts of the hills. It is not impossible that the distinction between the Malabar and Malay faunas has been intensified by their separation, due to the climate of Northern India having been too cold for them in the glacial epoch".

These authors thus attributed the spread of the Malayan forms to Peninsular India on two fundamental conceptions of Zoogeography– ecological succession due to Ice Age and subsequent isolation. In an article, not yet published, on "Himalayan Glaciation and its Effects on Terrestrial and Freshwater Animal life in India", I have shown that the Himalayan glaciation was not the controlling factor in the dispersal of the fauna and flora of Southern India and I am happy to say that several officers of the Geological Survey of India have now agreed with this view.

More recently, Smith (1931, p. 15 ; 1935, p. 15) referred to the Malayan affinities of the Peninsular fauna and asked "Why are they absent from Northern India ? Have they died out in that area, or was there at one time a more southern route across the Indian Ocean by which they could travel ?" Students of Indian geology and geography are aware that the Bay of Bengal is a fairly old feature of the physiography of India and from at least the commencement of the Tertiary Era (Fig. 4) there has been no southern route across the Indian Ocean connecting Peninsular India with Malaya. The second supposition of

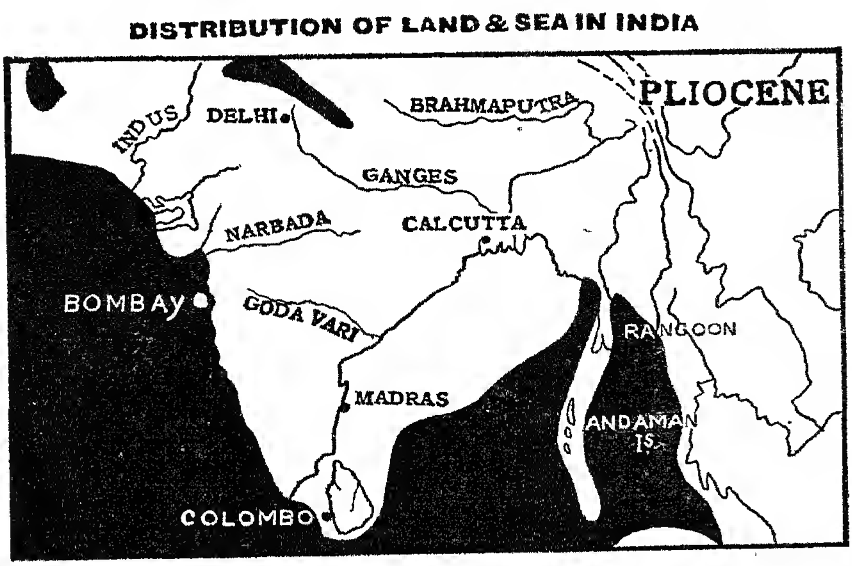

Fig. 4. Map showing the probable distribution of land and sea in India during the Pliocene period.
(Reproduced from a work of which the reference is lost).

Smith is, however, tenable; the Malaya nfauna has died out in the intervening regions. The question, therefore, arises as to what was its route of migration and what changes in the palaeogeography of India have occurred since which brought about the extinction of thisfauna in the intermediate regions.

It must here be remembered that, as remarked by Smith (1931, p. 15) in the case of Chelonians, true hill species "are of greater interest and value in the study of zoological distri-

bution than low-land forms. They are just as much isolated by the conditions under which they live as if they inhabited islands, and their occurrence on widely sparated mountain ranges is good evidence that a more direct connection between these ranges existed in the past times than is to be found today."

Attention may also be invited to a very significant remark of Medlicott and Blanford (1879, p. 375 foot-note) to the effect that "It is true that many of the temperate damp-loving forms of the Nilgiris and Ceylon hills are forest forms, and it may be urged that they might have migrated when the plains of India were covered with forest." They, however, dismissed this possibility in favour of refrigeration of climate, because they found it difficult to understand "how the plains of India can have enjoyed a damper climate without either depression, which would have caused a large portion of the country to be covered by sea, a diminished temperature which would check evaporation, or a change in the prevailing winds." They rightly dismissed the first and the third theories but wrongly accepted depression of temperature "the only remaining theory to account for the existence of the same species of animals and plants on the Himalayas and the hills of Southern India."

On an analysis of the above views, the following facts stand out most prominently, *viz.*, the continuity of mountain ranges between the *Stations* of present-day distribution of the Malayan forms and the presence of ecological conditions in the past in the intermediate regions similar to those now prevailing in their habitats. As early as 1937, to account for the distribution of hill-stream fishes I (p. 255) advanced the view that "The new stocks of specialised hill-stream fishes from the east, not finding means to cross this barrier, were deflected towards south-west along the Satpura Trend which probably at that period stretched across India as a pronounced range from Gujarat to the Assam Himalayas". Further investigations confirmed these views and I gave you a summary of the Satapura Hypothesis last year. Dr. J. B. Auden of the Geological Survey of India has very kindly

informed me that "the zone in the northern Peninsula between Chota Nagpur, and the Vindhya and Satapura ranges was periodically subjected to epeirogenic rise, sympathetically with the Himalayan movements, and may formerly have been at greater elevations than now, but that in more recent time denudation has removed a considerable thickness of rocks from these ranges." Computing from the existing geological structure of these ranges, he has surmised an elevation of 5,000 to 6,000 feet, *provided there has been no change in crustal elevation during the period of erosion.*

It is remarkable indeed that to produce climatic conditions similar to those of the Assam Himalayas and of the Malabar Tract, Dr. S. K. Banerji, Director-General of Observatories, computed that a height of 6,000 feet above sea level in the region of the Satpura and Vindhya Mountains will produce a precipitation of 150 inches annually. Such a heavy rainfall will naturally lead to thick, evergreen tropical forests which would have enabled the Malayan fauna to migrate to the Western Ghats. That immense forests, corresponding to the Terai forests of the present day, existed in these regions is also supported by the occurrence of elephants, *Hippopotamus* and *Rhinoceros* among the post-Pliocene Narbada fauna. These geological and meteorological observations have lent a great support to my Satpura Hypothesis of the distribution of Malayan forms to Peninsular India.

Conclusions

Zoogeographical studies on the Malayan forms found in Peninsular India have thus enabled me to build up the palaeogeography of the Satpura-Vindhyan ranges. They were during the Pletstocene as high as 5,000 to 6,000 feet and were continuous between the Himalayas and the Western Ghats. The rainfall in this region was 100 to 150 inches and they were covered with thick evergreen, tropical forests in which big game animals, such as elephants, rhinoceros and hippopotamus roamed about.

The ecological association, referred to above, has led me to

predict that there is every likelihood of these Pleistocene forests having been entombed in certain suitable places in the region of the Satpura-Vindhyan ranges, though some such deposits may now be thickly covered with the traps or other geological formations. If this surmise turns out to be correct, India has yet to discover its many rich deposits of coal and oil, which are so essential for the industrial advancement of the nation.

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stoma at the other. The sea level also fluctuated during the glacial periods, being lowest during the glaciation when large quantities of water were bound as ice near the poles. The Mediterranean at such times of lowest level was transformed into an inland sea and partially, if not completely, divided into two parts by the exposed land connection between Sicily and North Africa. H. Steinitz (1949) is inclined to suppose that the modern Mediterranean blennies are relics *in loco* of the Tethys in our region. But it must be kept in mind that, like most marine animals, blennies have pelagic larvae, which by passive locomotion could re-occupy an area lost in the past.

On the other hand there are, in fact, relics of the old fauna of the Tethys even in places where they would be least expected to survive: in fresh and brackish waters of the Anatolian plateau, as well as in similar biotopes in the regions around the Mediterranean which are nearly at sea level. I should like to draw attention to a family of small fish, the cyprinodontids. The genera *Cyprinodon* and *Aphanius* consist of some species in central and southern North America, and others around the Mediterranean and in central Anatolia, in the Dead Sea region, and finally in the western part of the Indian Ocean, including the Red Sea. Apparently this distribution as a whole corresponds to the western part of the Tethys. Everywhere these small fish live in such biotopes as marine coastal waters, the mouths of rivers, in lakes in the neighborhood of the sea, in fresh and salt springs inland, swimming freely in waters of very different salt concentration. As stated above, Anatolia, nearly at sea level in earlier geological periods, was elevated later. Cyprinodontids, having migrated inland, were thrust up with the rising Anatolian land mass. Because of their euryhalinity, they were able to survive in many places and today form one of the most characteristic groups in Anatolia and also in Palestine. It may be added that the enormous degree of variability with which we are confronted in the Anatolian cyprinodontids seems to be caused by interspecific or even intergeneric crosses in the past (Aksiray, 1952). Many of the populations of these fishes which at first sight look like different species, subspecies, or even genera are in reality, as it seems, nothing other than groups of a large hybrid swarm which in isolated populations have attained a more or less clear degree of uniformity; other populations are still heterozygous and composed of many different phenotypes.

It is probable that other survivors (Kosswig, 1943; Lohmander, 1939) of the Tethys are to be found among some of the subterranean genera of invertebrates around the Mediterranean and in Central America, including relatives of many marine forms of today. Such genera as *Caecosphaeroma, Monolistra,* and others may be mentioned. The transition of the ancestors of these cavernicolous forms to life in darkness was most probably accomplished by adaptation to specialized conditions of life in dark, cave-like places in the sea. Later, by the elevation of such formations rich in limestone, these forms became members of the subterranean inland fauna, without having passed through a stage of phylogenetic development in the superficial freshwaters of the continents.

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CURT KOSSWIG, now Professor of Zoology at the Zoological Institute, Hamburg, Germany, was Professor of Zoology at the University of Istanbul, Turkey, when this paper was written. The author adds: "The results presented above are, to a great extent, based upon new records obtained in the course of many excursions into different regions of Anatolia during 17 years. The material help liberally granted by the Rectorate of the University of Istanbul and the Decanate of the Faculty of Science facilitated these scientific trips. In the course of our travels we found the local State authorities of the greatest understanding and readiness to help whenever required. I wish to ~~express to them our grati~~tude in the name also of my collaborators who participated in these excursions. Wherever we came we were deeply impressed by the generous hospitality with which we were honoured even in the most remote villages of the country. Our task could not have been completed without the sincere interest shown by many private people all over Anatolia."

SATPURA HYPOTHESIS OF THE DISTRIBUTION OF THE MALAYAN FAUNA AND FLORA TO PENINSULAR INDIA.

By SUNDER LAL HORA, *D.Sc., F.R.S.E., F.Z.S., F.R.A.S.B., F.N.I., Director, Zoological Survey of India, Indian Museum, Calcutta.*

CONTENTS.

MALAYAN ELEMENT IN THE FAUNA AND FLORA OF PENINSULAR INDIA.

Distribution.—The existence of the Malayan element in the fauna and flora of Peninsular India has been known since a long time and efforts have also been made to explain the causes of these similarities. For instance, as early as 1879, Medlicott and Blanford (p. 374) observed:—

> 'On several isolated hill ranges, such as the Nilgiri (Noilghorry), Animale (Animullay), Shivarai (Shevroys), and other isolated plateaus in Southern India, and on the mountains of Ceylon, there is found a temperate fauna and flora, which does not exist in the low plains of Southern India, but which is closely allied to the temperate fauna and flora of the Himalayas, the Assam range (Garo, Khasi, and Naga hills), the mountains of the Malay Peninsula and Java. Even on isolated peaks, such as Parasnath, 4,500 feet high, in Behar, and on Mount Abu in the Aravali (Aravolli) range, Rajputana, several Himalayan plants exist.... In some cases there is a closer resemblance between the temperate forms found on the peninsular hills and those on the Assam range than between the former and Himalayan species, but there are also connections between the Himalayan and peninsular temperate regions which do not extend to the Eastern hills.... The animals inhabiting the Peninsular and Ceylonese hills belong, for the most part, to species distinct from those found in the Himalayan and Assam ranges, etc., in some cases even genera are peculiar to the hills of Ceylon and Southern India, and one family of snakes is not represented elsewhere. There are, however, numerous plants and a few animals inhabiting the hills of Southern India and Ceylon which are identical with Himalayan and Assamese hill forms, but which are unknown throughout the plains of India.'

Ecology.—In today's Symposium, we shall hear details of this peculiar fauna and flora from specialists interested in different groups of animals and plants, but you will notice that the ecological requirements of all Malayan terrestrial animals or plants found in Peninsular India are similar. It is remarkable that even this fact was recognized by Medlicott and Blanford who observed:

> 'The range in elevation of the temperate fauna and flora of the Oriental region in general appears to depend more on humidity than temperature, many of the forms, which,

in the Indian hills, are peculiar to the higher ranges, being found represented by allied species at lower elevations in the damp Malay Peninsula and Archipelago, and some of the hill forms being even found in the damp forests of the Malabar coast.'

Age.—It was pointed out by Medlicott and Blanford 'That a great portion of the temperate fauna and flora of the Southern Indian hills has inhabited the country from a much more distant epoch than the glacial period may be considered as almost certain, there being so many peculiar forms'. Though older than the last glacial epoch, this peculiar fauna and flora is perhaps not much older than the Early Pleistocene or Pliocene periods.

Torrential Fish Fauna.—So far as hill stream fishes of Malayan affinities are concerned, I (1944) gave a summary of the present-day knowledge before the Institute in 1944, and discussed the bearing of their distribution on the Garo-Rajmahal Gap. More recently I (1947) referred to the 'Torrential Fishes and the Significance of their Distribution in Zoo-Geographical Studies'. with special reference to the Homalopteridae. The ecological conditions favouring the distribution of hill-stream forms have been fully discussed in these articles and may be summed up as torrential, perennial, cool waters.

Crocodiles and Chelonians.—I (1948) recently placed before the Institute an account of the distribution of Crocodiles and Chelonians in Ceylon, India, Burma and Farther East, and showed that certain species of Peninsular India possess Malayan affinities. Concerning these reptiles, Smith (1931, p. 15) remarked:

'It seems equally certain that the Indo-Chinese hill tortoises, *Testudo elongata* and *Geoemyda tricarinata* did not extend their range into the Peninsula of India (Chota Nagpur) by crossing the Gangetic Plain. True hill species for this reason are of greater interest and value in the study of zoological distribution than lowland forms. They are just as much isolated by the conditions under which they live as if they inhabited islands, and their occurrence on widely separated mountain ranges is good evidence that a more direct connection between these ranges existed in past times than is to be found today.'

Lizards.—Smith (1935, p. 15) found similar anomalies of distribution in the case of lizards and stated:

'The close affinity which certain Indo-Chinese and Malayan lizards have with others that inhabit Southern India—the northern part of the Indian Peninsula being without them—raises an interesting point in zoological distribution. The resemblance which *Dasia olivacea* bears to *D. subcaeruleum*, *Lygosoma maculatum* to *L. dussumieri* and *Riopa bowringi* to *R. albopunctata* is so close that one feels convinced that if one has not been derived from the other they must surely have had a common ancestor. The genus *Draco* has a similar distribution; *Varanus salvator* occurs in Ceylon and in Indo-China, but is absent from the whole of the Indian Peninsula; and there are similar parallels in distribution among the mammals, birds, fishes and insects. Why are they absent from Northern India? Have they died out in that area, or was there at one time a more southern route across the Indian Ocean by which they could travel?'

[illegible].—In discussing the geographical distribution of snakes, Smith (1943, p. 26) remarked that 'In my volume on Lizards (p. 15) I commented on the affinities of the fauna of the Malayan Region with Ceylon and Southern India. Only one genus of snakes, namely *Cylindrophis*, has this distribution, being found in Malaysia, Indo-China, and Ceylon, but not in Peninsular India'.

Amphibia.—No recent work on the geographical distribution of Indian Amphibians is available, but reference may be made to the occurrence of the genera *Philantus*, *Ixalus*, *Kalula* and *Nectophryne* in Peninsular India and Ceylon on the one hand and the Malay region on the other.

In his recent article on the ornithogeography of the Gujrat Satpuras, Salim Ali (1948) has produced a mass of evidence in support of the Satpura theory and today he will himself place before all of you the relevant data. My colleague, Dr. M. L. Roonwal, will discuss the anomalies in the distribution of the Mammals similar to those I have referred above in the case of other groups of animals.

The occurrence of the Malayan element in the fauna and flora of Peninsular India is thus a widely recognized fact, but how this fauna and flora came to be so

dispersed and isolated are the important points that require elucidation. The following theories have so far been advanced to account for these anomalies in distribution.

THEORIES TO ACCOUNT FOR THE MALAYAN ELEMENT IN THE FAUNA AND FLORA OF PENINSULAR INDIA.

Himalayan Glaciation Theory.—Medlicott and Blanford (1879, p. lxx) attributed these anomalies in distribution to the temperature factor in the refrigeration of climate during the Ice Age. They stated:

> 'Among the most potent disturbing causes that have affected the fauna of India in late geological times, the general refrigeration of the area in the glacial-epoch has in all probability played a conspicuous part. The former extension of the Himalayan glaciers has been shewn to have been considerable; and the occurrence of Himalayan plants and animals on the higher ranges of Southern India may be due to the retreat of these species in the first place towards the equator, and subsequently, as the temperature increased, to the higher parts of the hills.'

This view is not tenable as already shown by me in 1944 (p. 430) in the case of torrential fishes and is contradictory to what Medlicott and Blanford had stated themselves about the age of this fauna and flora as being 'more distant epoch than the glacial period'. Recently (1949) I have dealt with this point in a separate article entitled 'Himalayan Glaciation and its effects on Terrestrial and Freshwater Animal Life in India' and shown that the temperature factor in Himalayan glaciation was not the controlling factor in the way indicated by Medlicott and Blanford in the dispersal of the fauna and flora of Southern India. The high humidities during the 'Pluvial' periods no doubt helped the distribution of animals, while the 'Arid' periods produced discontinuous distributions.

Southern Route across Indian Ocean Theory.—From our knowledge of the evolution of the geography of India, it is known that the Bay of Bengal has been a permanent feature, though in varying degrees, of the physiography of India since the commencement of the Tertiary period; so no southern route across Indian Ocean can be postulated. In a note on 'The Geographical Distribution of Indian Earthworms', Stephenson (1916) observed:

> 'The former connection by land of India and Australia, and India and New Zealand, is demonstrated by a comparison of the earthworm faunas; but it is not necessary to suppose, with Michaelsen, that the land connection must have extended across the Bay of Bengal; recent discoveries in the Abor country render it possible to suppose that the Oligochaeta immigrants took a path round the head of the Bay.'

Not only the Oligochaeta followed the route of migration round the head of the Bay but we shall presently see that for all groups of animals, aquatic and terrestrial, the path lay across the Assam Hills to the Vindhya-Satpura Trend of mountains to the Western Ghats and then down south to Ceylon. Land connections over the Bay of Bengal did not exist.

Deccan Traps Theory.—Though Stoliczka from his study of the distribution of birds suggested that the Deccan Traps may have been responsible for the discontinuous distribution of the Malayan element in the fauna of Peninsular India, Fr. Sarasin (1910) elaborated this suggestion into a plausible theory. It was recognized by him that the same genera occur at both ends but are represented by different species in South India and the Malay Peninsula and the Greater Sunda Islands. For specific differentiation in a continuously distributed fauna that became isolated into widely separated regions through natural causes, it has been estimated that a period ranging between 500,000 and one million years is sufficient, for very few species remain unaltered after a lapse of one million years. As has been explained in one of my other articles of this Symposium, the terrestrial fauna seems to have migrated in waves during the 'Pluvial' periods of the Pleistocene Epoch while

the aquatic animals were moving westwards over a much longer period, but not earlier than the Pliocene, a period of about 12 to 15 million years.

According to the present accepted views, the Deccan Traps commenced in the late Cretaceous and continued into the Eocene, a period of about 70 million years or more. It is obvious, therefore, that the Deccan Traps could not possibly influence the distribution of the forms under discussion here.

There is some zoogeographical evidence of the recent formation of the uppermost layers of traps, but this evidence has not yet been fully analysed and properly sifted to be of much use in the present discussion.

Continuous Range Theory.—This theory postulates that the various *Stations* at which a particular species is found at present once formed part of a continuous range of distribution of the species. It further postulates that in the regions in between the *Stations*, it has died out due to topographical changes leading to climatological variations and thereby in the ecology of the animal concerned. In a recent article on the 'Fundamental Conceptions of Zoogeography', I (1948*a*) have shown the principal factors that influence the distribution of animals. This theory can no doubt account for the anomalous distribution of the Malayan forms that are now found in Peninsular India but the chief zoogeographical interest lies in reconstructing the greatly obliterated route of migration of these forms between the Assam Hills and the Eastern Himalayas on the one hand and hills of the Malabar zone on the other. In 1937, while discussing the distribution of Himalayan fishes, I found that the specialized eastern hill-stream fishes had been obstructed in their dispersal by some unknown barrier in the Nepal Himalayas to the West of the Tista River and had thereby spread by a south-westerly route along the Vindhya-Satpura Trend of mountains which at that period stretched across India as a pronounced range from the Assam Himalayas to the Gujrat Western Ghats, whence the fauna spread southwards to the hills of Peninsular India and Ceylon. Objective field investigations and taxonomic studies have lent further support to this hypothesis and the facts are now so conclusive that all anomalies in the distribution of the Malayan fauna can be explained on the basis of the Satpura Hypothesis.

The Satpura Hypothesis.

The distribution of an animal or a plant is a static phase, for the dispersal of most of the species that exist today took place at a time when the geographical configuration of the country was very different from what it is today. The present-day distribution is thus the result of three phases in the past, namely, dispersal, establishment of the individual and finally establishment of the species. Let us take these three phases separately and discuss their implications with regard to the Satpura Hypothesis.

Dispersal.—It is generally known that most animal dispersal is directed towards ordinary feeding, breeding and other requirements of animals but not directly for the spreading of the species. In the case of aquatic animals, such as torrential fishes, there is the further disability of limited movements along set channels and in specialized habitats. Thus wide-spread dispersal of animals is usually the result of changes in the country's topography from time to time. In India, since the commencement of the orogenic movements that gave rise to the Himalayas and which were intensified in the late Tertiaries and Pleistocene periods, vast changes in the topography of the country have taken place. Dr. J. B. Auden has informed me that 'the zone in the northern Peninsula between Chota Nagpur, and the Vindhya and Satpura ranges was periodically subjected to epeirogenic rise, sympathetically with the Himalayan movements, and may formerly have been at greater elevations than now, but that in more recent times denudation has removed a considerable thickness of rocks from these ranges.' Computing from the existing geological structure of these ranges, he has surmised an elevation of 5,000 to 6,000 feet, provided there has been no change

in crustal elevation during the period of erosion. Thus one physical requirement for the dispersal of the Malayan fauna is satisfied—an elevated, continuous range of mountains from the Assam Himalayas to the Western Ghats. Probably due to the impact of the rising Himalayas with the ancient block of the Peninsula in the Assam region, produced waves along the Vindhya-Satpura Trend which dispersed the aquatic fauna from east to west through a series of river captures. The dispersal of the fauna, particularly aquatic, may thus be taken as partly due to mechanical causes.

Establishment of the individual.—The Malayan fauna having been dispersed mechanically through the topographical changes referred to above, the next point is the ecological specificity of the fauna. Even Medlicott and Blanford had recognized that this fauna 'appears to depend more on humidity than temperature' and opined that 'it is possible that the species common to Ceylon, the Nilgiris, and the Himalayas may have migrated at a time when the country was damper, without the temperature being lower'. Dr. S. K. Banerji has very kindly computed that if the height of the Satpuras were to be raised to 6,000 feet above sea-level, the annual rainfall on its slopes will be of the order of 150 inches according to the directions of the prevailing winds. Closely associated with rainfall will be the vegetation zones which will enable the moisture to be retained thus producing ideal damper conditions for the existence of the Malayan fauna. Today such conditions are found only on the top of hills, such as Parasnath Hill, Mount Abu, hills of Peninsular India and Ceylon and the forests of the Malabar zone, but when the Vindhya-Satpura ranges were 6,000 feet high with an annual rainfall of 150 inches, the intermediate regions had a uniform climate and harboured the damp-loving Malayan forms. With the denudation of the mountains, the once continuous distribution is now isolated into pockets having much damper climate than that of the intermediate regions.

Establishment of the species.—Ecologists are familiar with the fact that much abortive colonization is always taking place, partly owing to ordinary ecological factors being unsuitable and partly to the difficulty of finding a mate upon arrival at a new place. We have seen above that the ecological conditions were at one time favourable over vast areas and that owing to intense topographic changes the fauna was dispersed in large numbers. Thus the species had no difficulty in establishing themselves after dispersal. It may here be noted that after dispersal over a wide area and particularly after isolation into particular *Stations*, the fauna began to show variations in different directions resulting in the evolution of new races, subspecies, species and even genera, but the characteristics of the Malayan affinities have remained deeply impressed on their morphological and physiological organizations.

Conclusions.

The Satpura Hypothesis of the Distribution of the Malayan Fauna and Flora to Peninsular India is thus based on the following fundamental conceptions:—

(1) Continuity of the Vindhya-Satpura ranges with the Assam Himalayas in the east and the Western Ghats in the west.

(2) Five to six thousand feet elevation of the Vindhya-Satpura ranges and of the northern section of the Western Ghats.

(3) Continuity of an ecological belt of mountains with rainfall of about 100 inches or above and consequently of the tropical evergreen forests between the Assam Himalayas and the mountains of Ceylon *via* the Vindhya-Satpura Trend and the Western Ghats.

(4) Dispersal of the fauna from east to west and the consequent changes in topography necessary therefor.

Sufficient evidence now exists in support of each one of these conceptions and more and more facts are coming to light as the subject receives further attention.

I have received great help and encouragement in my studies on the zoogeography of India from the officers of the Meteorological Department (Dr. S. K. Banerji, Dr. K. R. Ramanathan, Dr. V. V. Sohoni and Dr. L. A. Ramdas), from the officers of the Geological Survey of India (Dr. A. M. Heron, Sir C. S. Fox, Dr. W. D. West, Dr. D. N. Wadia, Mr. V. P. Sondhi, Dr. J. B. Auden and Dr. K. Jacob) and Professor H. L. Chhibber, Professor of Geography, Banaras Hindu University. I am most grateful to all of them. They are all, however, busy with their own studies or administrative duties, and can only spare little time to my manifold enquiries on zoogeographical matters. The subject I have placed before you today needs much further investigation and intensive study from all aspects by a special team of scientists. Such a study, if properly pursued, will lead to many new facts concerning the geography and geology of India.

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A GEOLOGICAL DISCUSSION ON THE SATPURA HYPOTHESIS AND GARO-RAJMAHAL GAP[1]

By J. B. AUDEN, Sc.D., F.N.I.

CONTENTS

I. INTRODUCTION

Recent studies by Dr. S. L. Hora on the migration of freshwater fish, crocodile, and Chelonian faunas have led him to postulate the possible former existence during the Tertiary era of a mountain range extending from the Shillong plateau, across the Rajmahal gap, westwards to the Vindhya-Satpura region, along which migration is thought to have taken place. The Garo-Rajmahal gap is considered to have been of recent formation and to have blocked the further migration of the Eastern Malayan fauna (Hora, 1944, p. 433; 1948, p. 305). The following note is concerned with the available geological evidence pertaining to the former existence of the Satpura Range and the dating of the Rajmahal gap. Considerable discussion by geologists and others followed Dr. Hora's paper of 1944, while Dr. Tindell Hopwood submitted certain generalizations about the Satpura range in 1948.

To make a satisfactory study of this problem would involve a comprehensive review of all geological processes that have occurred in northern India since the beginning of the Mesozoic era, and would take much more time and research than is possible with other pressing commitments. Consequently, only a relatively cursory review can be undertaken in this paper, without a full consideration of all the literature. It may be pointed out that the opinions expressed herein are my own, and do not necessarily represent those of the Geological Survey of India.

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At the outset it should be emphasized that the problem of earth movements, and changes of land relative to sea-level, is one that is highly involved. Not only is it necessary to consider the effect of earth movements along the mobile orogenic belts, and epeirogenic changes in the more extensive crustal blocks, both arising from stresses indigenous to the planet, but attention in some areas has also to be paid to extraneous changes in the level of land relative to sea caused by the superimposed loads of great ice caps, involving in addition the periodical locking up of immense quantities of water in the form of ice caps and its subsequent release as the ice melted. Moreover, movements must be considered in relation to the principle of isostasy, or the delicate balance which exists over most parts of the planet between the crust, of varying thickness and density, and the weak supporting asthenospheric shell. Erosion in elevated regions removes part of the superficial crust and redeposits the material elsewhere, so that the crustal balance is upset, and adjustments in elevation take place if restraints from other causes are not present.

In actuality, adjustments do not take place at once. Along the orogenic belts in particular there may be prolonged departures from isostasy in narrow zones characterised by high positive or negative gravity anomalies (Vening Meinesz, 1934; Hess, 1938). These narrow zones of gravity anomalies are considered to be due to the existence of stresses in the crust and underlying asthenosphere which have prevented the crust from attaining equilibrium in a vertical sense with the weaker shell below. Even in the more stable epeirogenic regions of the crust there may also be considerable departures from isostasy, though not of the same magnitude as in the mobile orogenic belts.

As an example of the sensitivity of the crust to newly acquired loads, and the subsequent removal thereof, may be mentioned the giant ice cap which occupied approximately 1·2 million square miles of north-east Europe during the ice age (the area of the Indian Union), and at the time of the maximum development may have reached a thickness of 10,000 feet in the centre. This was an additional load which had the effect of depressing the crust into the asthenosphere.

The melting of this ice cap, which is equivalent to the removal of 3,700 feet of rock of density 2·7 in the central region, has resulted in the gradual rise of the land since the end of the last glacial phase. The maximum rise in land took place on the west side of the Gulf of Bothnia, near Lat. 64° N.: Long. 21° E., where the elevation has been of the order of 2,300 feet, and as much as 1,700 feet during the last 9,000 years (Daly, 1940, p. 313). This is equivalent to an average annual rate of rise of 5·7 cms., though it should not be supposed that the rise has been at a uniform rate since its inception.

In considering, therefore, the removal of masses by erosion in a manner analogous to the melting of an ice sheet, it is not possible to regard a given quantity of rock, corresponding to a known vanished stratigraphical succession, as merely worn away from the earth's surface, and therefore only to be added to the present land height so as to provide a figure of the original height of the land before erosion began. The very fact of erosion upsets the isostatic balance of the crust, and results in a compensatory elevation of the crust provided other restraints do not exist. The net effect of erosion over a long period of geological time is therefore to cause an elevation of the crust, though not necessarily to the same level as originally obtained, just as the melting of an iceberg causes the whole mass of the berg to rise in the sea until it eventually melts entirely away. Consequently, it follows in general that the net change in elevation of the crustal surface is less than that which is implied by the actual subtraction of material eroded away.

It is necessary in a study of this problem also to consider recognized stratigraphical horizons, the manner of formation of which is known to within fairly definite physiographic limits. As far as possible, it is desirable therefore to know the palaeogeographical conditions which obtained at the time when given formations were deposited: in which direction lay the highlands that acted as a provenance to the

formations being deposited, and the orientation of the main river systems acting as media for deposition.

One major uncertainty exists in the lack of knowledge as to how far given formations formerly extended beyond their present outcrops. This uncertainty naturally affects any calculations based on quantities of rock removed by erosion, and the attendant modification considered above, of isostatic adjustment arising from re-distribution of crustal loads.

Finally, the present level of crustal masses as now exposed is the net effect of all the vertical movements of positive and negative sign which have taken place during the period since given formations were deposited. In certain areas there may have been a complex sequence of subsidence and elevation, the decipherment of which, in the absence of certain key formations removed by erosion, may be very difficult.

II. The Ur-Satpura Range

The term *Ur-Satpura* is used in this paper to describe the possible ranges, or more elevated plateaux, which on this hypothesis extended during the late Tertiary from the northern end of the present Western Ghats in an easterly direction to the present Rajmahal Hills, that is, between longitudes 74° and 88° and latitudes 21° 30′ and 25°. It includes, therefore, the modern Satpura Range rising between the Narbada and Tapti rivers, the Mahadeo Hills or Satpuras near Pachmarhi, the Maikal and Mainpat Hills, and the Chhota Nagpur plateau. Across the present Garo-Rajmahal gap it includes the Garo and Khasi Hills of the Shillong plateau. The first part of this discussion will be confined, however, to the area in the mainland of India between the Western Ghats and the Rajmahal Hills. A later section will discuss the Garo-Rajmahal Gap.

1. *Present Surface Elevations*

I am indebted to my colleague, Mr. A. K. Saha, for the elevation data summarized in Table 1. This list includes only certain representative summits and is

Table 1.

	Average elevation of plateau	Highest individual summit	Range in elevation of selected summits on plateau
Parasnath		4,480	
Ranchi East	1,800–1,900	3,517	
Ranchi West	2,200		3,445–3,517
Hazaribagh	1,900	3,200	2,569–3,200
Mainpat	1,800–2,000	3,781	3,476–3,781
East of Ambikapur		3,800	3,283–3,800
Sohagpur Highlands	2,000–2,250 rising to nearly 3,000 in East.	3,651	3,299–3,651
Mandla Highlands..	2,000–2,250	3,065	2,732–3,065
Chhindwara and Pachmarhi	2,000–2,250	4,429	3,481–4,429
Mhow	1,800–1,900	2,891	....
Gawilgarh	2,000–2,500	3,682	3,486–3,682
Satpura, Indore	2,000–2,250	3,522	3,219–3,522
Satpura, Barwani-Bombay	1,800–2,200	4,347	3,274–4,347
Indore Plateau	1,700–1,800	2,451	
Bhopal	1,500–1,700	2,107	
Kotah	1,250–1,500	2,014	1,775–2,014
Panna	1,300–1,400	2,178	1,797–2,178

not to be regarded as a complete indication of height variations. The present elevation of the tract varies from about 200 feet on the east side of the Rajmahal Hills to 4,480′ at Parasnath. The greater part of the inland area consists of plateaux varying within the small limits of 2,000 and 2,500 feet. Sticking up out of these plateaux are higher plateaux and residual summits which average about 3,500 feet and have individual summit variations of only about 300 feet. Exceptional heights include Parasnath 4,480′, Dhupgarh 4,429′ near Pachmarhi, and one peak in the Satpuras south of the Narbada of 4,347′ feet. These heights presumably represent residuals of the highest original plateau, most of which has been completely removed by erosion. Between the Highlands occur the Narbada and Tapti valleys with average elevations of about 1,000 ft. in central India.

2. *Geological Structure*

A glance at the geological map of India shows that the east-west zone of the Ur-Satpura Range includes a great variety of geological formations, which are tabulated below:—

7 Older alluvium and Siwaliks of the Tapti and Narbada Valleys.
6 Deccan Traps of Rewa Kantha, Bombay, Barwani, Gawilgarh, Mahadeo Hills and the Maikal Range.
5 Rajmahal Traps of the Santhal Parganas.
4 Upper Gondwana formations of the Mahadeo and Deogarh Hills, and small outliers in the eastern coalfields.
3 Lower Gondwana formations of the Mahadeo and Deogarh Hills, Surguja, the Damuda rift valleys of the Chhota Nagpur region, Rajmahal Hills.
2 Vindhyan Formations of Bhopal, Saugor, Rewa and Mirzapur.
1 Archaean formations of the Hazaribagh Range extending eastwards to the Rajmahal Hills.

This area, which has to be considered in the light of the Satpura hypothesis, is therefore geologically complex. Aside from the intensely folded and often highly metamorphosed Archaean rocks, the changes in which are not relevant to the present enquiry, the remainder of the formations listed above show only moderate to slight folding. Over large areas the sedimentary and volcanic formations lie with virtual horizontality, pronounced folding in them being confined to narrow zones, such as the crumpled and faulted Vindhyans in Bundi and along the Son Valley (Coulson, 1927; Auden, 1933) and the flexures in the Upper Gondwanas bordering the Narbada Valley (Crookshank, 1936). The greater part of the Deccan Traps are unfolded, but the western end of the Satpura range includes the folded traps of Rajpipla first described by Blanford. The dyke clusters and swarms in the Deccan Traps appear to be closely related to this somewhat abnormal folding to which these traps have succumbed along the Narbada zone (Blanford, 1869, p. 57; Auden, 1949, p. 132). The Lower Gondwana rocks of the eastern coalfields have, however, undergone considerable folding, in particular in the Jharia coalfield, and the high fuel ratios of some of the Barakar coals, in places removed from the thermal effects of mica-peridotite intrusions, is indicative of considerable stress.

The characteristic feature of the Gondwana rocks is the strong faulting which has let them down into troughs in the Archaeans. This is well displayed in the Bokaro coalfield which lies in depressed ground 1,000 feet lower than the flanking elevated Archaean plateaux of Ranchi and Hazaribagh. In several fields the faulting is pronounced only on the south side, and in the Jharia and Raniganj coalfields there is an échelon arrangement of the southern boundary faults.

At the eastern edge of the Gondwana rifts there is a convergence below alluvium of three distinct radiating patterns of down-faulted Gondwanas towards an area near co-ordinates 23° 35′ : 87° 45′, close to Bolpur, represented by the Damodar

rifts, the radiating outliers of the Giridih group, and the Gondwanas of the western side of the Rajmahal hills. This converging fracture pattern which broke up the Archaean basement must have reached final development at the close of the Gondwana period or in the early Tertiary.

Between the Raniganj and Hutar coalfields, the coal-measures now follow an east-west system of troughs, although individual boundary faults lie oblique, and en échelon, to the main east-west zone. This east-west pattern continues westwards, being characterized by the elongated outcrop of Upper Gondwanas, synclinally lying upon Lower Gondwanas, which extends to Janakpur and Bandhogarh. Still further west this strike swings round to E.N.E.-W.S.W., and follows the structural feature which is dominated by the Narbada rift.

A tentative schematic representation of the crustal blocks in India during the Tertiary era is given in figure 2. The Peninsula is regarded as being divided into a northern or Aravalli shield, and a southern or Deccan shield, by a pronounced line of weakness which runs along the Narbada and may continue E.N.E., north of Monghyr, to form the northern boundary of the Shillong mass. This Narbada zone is considered to be an ancient feature connected with some primary weakness parallel to the Archaean grain and related in the west to an upwarp of the asthenospheric shell into the superficial crust. The peninsular Gondwana rocks, which have been dropped down along rifts and unilateral tensional faults, are confined to the southern shield (see also Fox, 1931, Plate 10).

The elevated land which might be considered to be the remnants of the original Ur-Satpura range lies along the northern edge of the southern shield and cuts obliquely across all the lines of weakness and fracture which developed in the Mesozoic and reached final emphasis at the close of the Gondwana period. In the eastern part of the Ur-Satpura it is not possible to think in terms of a Range in the sense that the Aravalli Hills and parts of the Himalaya form ranges, for there is no correspondence between structure and the present line of highlands. It is necessary, therefore, to consider the problem mainly in terms of an Archaean basement, broken up by lines of late-Gondwana weakness, that has existed as plateaux undergoing vertical movements of negative and positive sign during the Tertiary and post-Tertiary areas.

3. *Geodetic Evidence*

The gravity anomalies determined by the Survey of India have been developed in the form of a map showing the Crustal Structure Lines of India (Glennie, 1937). These lines are intended to show zones of upwarp and downwarp, after corrections have been made of the observed values of gravity for latitude, altitude, the attraction of neighbouring masses, and some degree of isostatic compensation. They include the effects both of deep sedimentary basins containing rocks with abnormally low density, and zones of upward buckling of the asthenospheric shell (without prejudice regarded as basalt) into the granitic crust. It should be stressed that these so-called downwarps and upwarps are not necessarily represented by corresponding topographical features. One conspicuous downwarp runs through the southern line of peaks in the Karakoram range, which has more peaks over 7,000 metres in elevation than any other region of the world. The major upwarp west of Bombay runs under the Arabian sea and hits the coast of India in the low-lying Gulf of Cambay.

This map has, indeed, led to misunderstandings, and it has been excluded from recent publications of the Geodetic Branch of the Survey of India. The line of the hypothetical Satpura range may, however, be examined in the light of the Crustal Structure map. The Ur-Satpura range starts along the zone of upwarp which runs between the Narbada and Tapti valleys. It continues over the junction of two zones of downwarp which exists near the Mainpat Hills in Surguja and Udaipur,

and then strikes obliquely towards the major upwarp which extends from the Shillong Plateau across the Rajmahal gap to Allahabad and Agra.

Except in the western part of India, where upwarp coincides with the Satpura range between longitudes 74° and 76°, the hypothetical Satpura range of antiquity runs oblique to the crustal structure lines as indicated by gravity anomalies. Consequently, the existence of the Ur-Satpura has little support from the basic structural relationship between the superficial crust and the underlying asthenospheric shell.

From considerations of the evidence from both geological and geodetic sources, we are compelled therefore to regard the problem as connected mainly with epeirogenic movements which have depressed and elevated extensive areas of the peninsula, irrespective of both geological strikes in the superficially exposed crust and deep-seated warps which have affected the level of the interface between the base of the granitic crust and the underlying asthenospheric layer.

4. *Key Horizons*

A description of the sequence of earth-movements which affected northern India is given by D. N. Wadia, J. A. Dunn and the writer in the account of the Bihar-Nepal Earthquake of 1934 (1939, pp. 118–160). Of particular importance is Dunn's account of the movements during the Tertiary era which took place between Chhota Nagpur and the Rajmahal Hills (1939, pp. 137–142). There is also information in Crookshank's survey of the Satpura region around Pachhmarhi (1936, p. 376).

Dunn has indicated three base lines which provide evidence regarding vertical movements:—

(1) The base of the Gondwanas;
(2) The base of the Deccan Trap and Rajmahal Trap;
(3) The coastal Tertiary deposits.

In addition, may be added two other formations which throw some light on the problem:—

(4) Base of the Eocene;
(5) The older alluvium, and Siwalik rocks, of the Narbada and Tapti valleys.

Another key formation is found in the glauconitic sandstones of the Lower Vindhyan Semri series (Auden, 1933, p. 212), but uncertainty arises in attempting to unravel the vicissitudes of vertical movements which these ancient rocks have undergone during the course of the approximate 400–500 million years since the beginning of the Palaeozoic.

5. *Base of Gondwanas*

The exposed base of the Gondwanas rises from an elevation of about 200 feet in Bengal to almost 3,000 feet near Sohagpur and Chhindwara though, where depressed by synclinal folding and downfaulting at the bottom of the coalfield troughs, the base must be several thousands of feet below sea-level in Bengal. At the time of deposition of the Talchir tillite, the Gondwana continent must have been more or less devoid of pronounced topographical interruptions, since the tillite of the Salt Range contains boulders derived from the central parts of India, and the ice sheet evidently spread without intervening elevations which would otherwise have caused deflection of boulders from central India away from what is now the Salt Range. The highlands from which the ice sheet spread are considered to have been in the south, and probably south of the present Satpura trend.

The Talchir beds of Umaria (23° 32′ : 80° 50′) are associated with marine beds containing *Productus* (Cowper Reed, 1928, p. 367) and it is clear that these particular glacial beds must have been deposited at and just below sea-level. The

present elevation of the outcrops at Umaria is about 1,500 feet. There is evidence that the later coal measures were deposited by an extensive river system which flowed westerly from highlands that lay to the east and south (Fox, 1931, Plate 10).

Since the available evidence suggests that the highlands lay to the east and south, and since the eastern parts of the outcrops are now at much lower elevations than those in central India, it is probable that there has been a rise of some 3,000 feet in central India relative to Bengal. In view of the isostatic rise that has taken place in Scandinavia since the melting of the Pleistocene ice sheets, it is possible that a similar adjustment occurred on the melting of the Talchir ice sheet at the beginning of the Permian. This rise should have been greatest where the ice sheet was thickest, which was by inference in south-central India. Consequently, the topography of Gondwanaland may have changed slightly during the deposition of the coal measures, but not in such a way as to reverse drainage profiles. Indeed, the isostatic rise would tend to restore the original gradients, which were responsible for the radial movement of ice from the centre of the ice sheet, and which were presumably lessened during the period of maximum glaciation as a consequence of the superimposed load of ice. As will be discussed later, however, the greater part of the differential elevation of the Gondwanas between Bengal and central India probably took place after deposition of the whole Gondwana succession and its downfaulting into troughs.

A tillite, almost certainly of Talchir age, is also found sporadically in the outer Himalaya between longitudes 77° and 95°, over a distance measured along an arc of 1,300 miles. In the Simla-Mussoorie region it is associated with a characteristic pink siliceous dolomite, and in Nepal with massive white dolomite and coaly shales (Auden, 1934, p. 374; 1946, p. 346). It was evidently laid down close to the shore line of the sea in which the non-fossiliferous Peninsular-Himalayan rocks were deposited. Present outcrop elevations vary from about 7,000 feet in the Simla region to 370 feet on the banks of the Kosi river in Nepal. There would appear, therefore, to be a larger elevation of these rocks in the neighbourhood of longitudes 77°–82° than east of longitude 86°, in a comparable manner to what is indicated for the Lower Gondwanas of the Peninsula proper.

Finally, may be mentioned the rocks of glacial or fluvioglacial origin which are found at an elevation of 19,500 feet across the main Himalayan range in north-east Sikkim (Wager, 1939; Auden, 1946) and in the Horpatso region of Tibet, at geographical co-ordinates 34° 33′ : 81° 8′ (Norin, 1946, p. 75). These rocks occur at elevations of 18,000 to 22,000 feet. The relationships, however, between the trans-Himalayan glacial beds and those belonging to the Peninsular-Himalaya and Peninsula proper are not at present understood. The Tibetan rocks described by Norin may, in fact, belong to the Angara crustal block, and not to Gondwanaland.

6. *Base of the Deccan Traps*

The base of the Deccan Trap varies within considerable elevations. It is at sea-level 60 miles N.N.W. of Marmagoa and 2,000 ft. above sea-level at Belgaum, only 75 miles away. This particular change in elevation may be connected with the Panvel flexure of post-Deccan Trap age (Auden, 1949, p. 148). East and north-east of Belgaum towards Nagpur the base varies within the approximate limits of 1,000 and 2,000 ft. South of Pachmarhi it is 3,000 ft. Along the south flank of the Maikal range it follows roughly the 500 metre contour (1,640′) but rises to about 2,500 ft. south of Sohagpur. Finally, an outlier in Jashpur, at the south-west end of the highest plateau of the Hazaribagh plateaux, lies at over 3,000 ft. The base is therefore not at all uniform. In certain areas, such as Cutch, Gujerat, and the west side of the Konkan, the traps are considerably folded, but over the greater part of the main Deccan plateau they are, so far as is reported, virtually unfolded and horizontal. It is not possible to assume, therefore, that the irregular floor

over most of the trap outcrop is due to folding, for the irregularity is evidently that of the original topography upon which the lava flows were erupted. This has been well described in the Pachmarhi area by Crookshank (1936, p. 276) and by Ball in the Rajmahal area (1877, pp. 59, 60). As I have recently pointed out, the Deccan Traps deserve much more detailed study and it is possible that gentle warps may be found to be more common than is now supposed. But the general conclusion remains true, that the floor upon which the traps were laid down was uneven, and varied usually within a height range of 1,000 feet. The subsequent warps will have tilted the traps together with the local declivities of basement topography.

7. *Nature of the Deccan Trap Floor*

It is necessary now to consider the structural relationships of the traps with the rocks upon which they lie. It is quite evident that there is a very strong unconformity upon the Vindhyan and Gondwana rocks. South of Kotah, near Jalrapatan, and east and south of Saugor, the traps cut across the various subdivisions of the Vindhyan system with a violent discordance. This discordance is very well displaced in south-west Mewar (Heron, 1936: Plate 22).

The full thickness of the Vindhyan system is developed only in central India, near Hoshangabad and the Dhar Forest, where possibly 10,000 to 13,000 feet of sediments are present. Eastwards the upper series of the Vindhyans disappear, and in Mirzapur district (Mallet, 1869; Auden, 1933), and Shahabad district, only the Semri and Kaimur series are exposed. If the Rewa and Bhander series were formerly present in the east, as appears to be very probable, they have now been eroded away, and at least 4,000 feet of sediments are missing. When the problem of the Satpura range was first put to me by Dr. Hora, I had myself argued that the removal of over 4,000 ft. of sediments might, after allowance was made for isostatic rise, account for the former existence of a higher plateau. At that time, however, the regional geological map had not been studied in detail, and the significance of a highly titaniferous bauxitic laterite on the Rohtas plateau (24° 44′ : 83° 58′), at an elevation of 1,600 feet, which was examined in 1939, was not appreciated. As was pointed out above, Deccan Trap outliers occur at a high elevation on the Hazaribagh plateau, only 100 miles south of Rohtas, and numerous outliers exist between Rohtas and Ambikapur. The titaniferous bauxite, with 6·95% of TiO_2, is almost certainly not derived from erosion of the Kaimur sandstones upon which it rests, which lack titanium. It is much more likely to represent the last residue of weathering of an outlier of Deccan Traps resting on the Kaimur sandstone. The former extension of the Deccan Traps into Ranchi District was inferred in 1923 by Fox from the widespread deposits of bauxite found on the high plateau of that area, one major deposit being at Bagra Pat (23° 29′ : 84° 36′). The case is therefore strong for assuming that the Deccan Traps at one time covered Vindhyans and Archaeans alike in this region at least as far east as longitude 85°. This is 190 miles beyond the main existing outcrop. If, therefore, the Deccan Traps formerly rested unconformably upon the Kaimur sandstones of Shahabad, the erosion of the Rewa and Bhander series must have taken place in pre-Deccan-Trap times, and the removal of these sediments would not be relevant to the Ur-Satpura hypothesis. The unconformity would be merely another example of what is still so well displayed in central India, near Jalrapatan, Saugor and south-east Mewar (Fig. 1).

More significant than the Deccan-Trap/Vindhyan unconformity is, however, the unconformity between the Deccan Traps and the Gondwana rocks. The traps and underlying Lametas (Infra-Trappeans), cut across all the exposed members of the Gondwanas south of Chanda and Pachmarhi, and in the neighbourhood of Sohagpur. Further, outliers of traps occur between Sohagpur and Janakpur, and again south and east of Ramkola, resting across the boundary between the Upper and

Lower Gondwanas. This clearly indicates that the folding of the Gondwanas was completed before the eruption of the traps. Crookshank has shown, for example, that the main unconformities in the Pachmarhi area are below the base of the Jubbulpore series (Middle Jurassic) and below the Lametas (Upper Cretaceous). The Deccan Traps, regarded as Eocene on the basis of fossils found in the inter-trappeans, and the sporadic underlying Lametas, overlap almost the whole of the Gondwana succession within a distance of 26 miles (1936, Plate 25). The earth movements in this area took place therefore during the Jurassic and Cretaceous periods.

Coming to the Rajmahal area in Bengal, it may be noted that the Rajmahal Traps, of Lower Jurassic age and 1,500 to 2,000 feet in thickness, have gentle dips to the east, but this tilting probably took place during the Tertiary. Aside from this very gentle tilting, no folding has occurred in this region since the Lower Jurassic (Blanford, 1861, p. 144; Ball, 1877, p. 66). Unconformities occur between the Barakars and Dubrajpur Beds (Upper Gondwana), and between the latter and the overlying Lower Jurassic lavas, and the compressional movements were completed therefore by the end of the Trias. The major N.N.W.-S.S.E. faults forming the western boundary of the Gondwanas of this area are post-Mahadeva, but no contacts are seen with the traps and an upper age limit cannot be given. Hobson has, however, found that the Jurassic lavas, and the igneous intrusions (of either Jurassic or Deccan age), are affected by faulting, and the latest faulting must have been at a much later age, perhaps towards the close of the Deccan episode (Hobson, 1930, p. 145; Fox, 1934, p. 55).

8. *Base of the Eocene in relation to the Traps*

In the Cutch area, on the other hand, there is a negligible unconformity between the mainly Cretaceous Deccan Traps and the underlying Cretaceous and Jurassic rocks. Significantly, however, a very pronounced unconformity exists between the Lateritic and Nummulitic rocks (pre-Laki and Laki, or middle Eocene) and the underlying Deccan Traps, Cretaceous and Jurassic. The so-called sub-Nummulitic rocks or laterities overlap across the traps south of Lakhpat on to Upper Jurassics, while in the outlying areas of Rapar, Patchham and Bela, they rest against Lower Jurassic or Bathonian, without any intervening traps. It is not possible to enter into a discussion regarding the age of the Deccan Traps in this paper, but it is likely that the traps of Cutch are older than those of much of the mainland of India (Auden, 1949, p. 149) and that the earth movements which caused the erosion, lateritization and unconformities took place after the eruption of the Cutch traps, but before that of the eastern Deccan traps, possibly in Lower Eocene or Ranikot times.

Similarly, both east and south of Broach, the Eocene lies against Deccan Traps (Blanford, 1869, p. 62; Bose, 1908, p. 174). Descriptions of this region are not detailed, but Blanford gives convincing evidence for an erosional unconformity and divergence of strike between the Nummulitics and the underlying Deccan Traps near Uskar, 4 miles south-east of Tarkesar. He also describes the traps near Ratanpur (21° 43′ : 73° 11′) in Rajpipla as having a southerly dip of 10° and being overlain by Tertiaries dipping west and N.N.W. Bose, on the other hand, indicates that the anticlinal fold of the Tertiaries between Ratanpur and Damlai has an east-west axis (1908, p. 175), which is more or less coincident with the E.N.E.-W.S.W. strike of the fold axes of the Deccan Traps lying to the east. These particular traps in Rajpipla are considerably folded, and between latitudes 21° 10′ and 21° 45′ are infested with swarms and clusters of dykes (Blanford, 1869, p. 58; Auden, 1949, p. 132 and Plate 8). Both Blanford and Bose agree that the Nummulitics rest upon an eroded surface of the traps, and Bose states that the materials from the traps to some extent made up the composition of the Tertiaries. In this point he

is evidently referring to the agates and cornelians which occur extensively as pebbles within the Upper Tertiaries of Ratanpur, but he implies that a few such pebbles also occur in the Lower Tertiaries which immediately overlie the traps. Oldham (1893, p. 300), referring more particularly to the Lower Tertiary Nummulitics cropping out on the banks of the Tapti river about 18 miles east by north of Surat, mentions that interbedded with the nummulitics occur conglomerates containing pebbles of agate. He also stresses that there is a distinct unconformity between the Lower Tertiaries and the Deccan Traps. The fauna of the Nummulitics is a mixed Ranikot-Kirthar type.

Unfortunately, no detailed geological mapping on large scale maps has been done in this area, and the Upper and Lower Tertiaries have not been properly differentiated. But the evidence so far adduced, and the general north-south strike of the boundary of the Lower Tertiaries against the underlying Deccan Traps, which were folded along E.N.E.-W.S.W. axes and intruded by swarms and clusters of dykes parallel to the fold axes, suggest that there is an abrupt truncation of the trap folds by the Nummulitic and later Tertiary rocks. There is no record of any of the E.N.E.-W.S.W. dykes intruding the Tertiaries, and the probability arises therefore that both the folding of the traps and the intrusion of dykes took place before deposition of the Eocene rocks. This critical area deserves further attention.

These relationships in Cutch and Gujerat are in striking contrast to those which obtain in east-central India where, as already noticed, the Gondwana earth movements were consummated, and extensive erosion had occurred, before the traps were erupted. The evidence obtained by B. Sahni, S. L. Hora, H. Crookshank and others suggests that most of the inter-trappean horizons of the Peninsula are of Eocene age. It follows therefore that the earth movements which folded the Gondwanas (and possibly caused rejuvenation of folding along old Vindhyan axes) could not have been later than the beginning of the Eocene. Indeed, the evidence of unconformities indicates that most of the movements resulting in folding and erosion of the Gondwanas were completed in the Mesozoic era. It is true that S. L. Hora has considered on other grounds that the youngest Deccan Traps may be much younger than Eocene (1947, p. 10; 1949, p. 305). If the traps of eastern India which unconformably overlie folded and eroded Gondwanas are proved to be of mid-Tertiary age, and if no Cretaceous Lametas are present below them, the final folding and erosion of the Gondwanas might be placed later than Eocene. So far as fossil evidence goes, however, there are not sufficient reasons for believing that the traps are younger than Lower Tertiary, and we are compelled therefore, both on these grounds and on the nature of unconformities in the Gondwana rocks, to regard the final folding of the Gondwanas as Cretaceous. In the Rajmahal area it was even earlier and probably Triassic. The downfaulting which took place in the Bokaro, Jharia, Raniganj and other coalfields was later, but an upper age-limit cannot be assigned to these displacements. Heron (1938, p. 128) indicates that the rejuvenation of the Aravalli Range, by as much as 3,500 feet in the centre, involved uplift along the Great Boundary Fault. Since this fault is truncated by flat-lying Deccan Traps, the movement was probably completed by the end of the Mesozoic, and may be related to those which affected the Gondwana rocks.

The important point in regard to the Ur-Satpura hypothesis is that these earth movements of compressional type, whether Mesozoic or Lower Eocene, were followed by erosion and the subsequent covering of the Gondwanas by unfolded lavas. Indeed, the very gently tilted Rajmahal traps of Lower Jurassic age prove that no compressional movements took place in the Bengal area since the end of the Triassic. Mid-Mesozoic compression was followed by tension, which evidently began in eastern India during the Lower Jurassic and continued right up to the middle of the Tertiary era, when it was finally succeeded by compression. As the hypothesis requires the existence of a range in Upper Tertiary times, this period of pre-Rajmahal and pre-Deccan Trap folding can have no bearing on the existence of the range. Indeed,

the later the age of the Deccan Traps, as now proposed by Hora, the more damaging is the fact of their eruption under tensional conditions to the hypothesis, which is concerned with post-trappean movements. For, as will be seen below, the ecological evidence is that the inter-trappean beds were deposited close to sea-level.

The greater part of the extensive Deccan Trap outcrop, 200,000 sq. miles in area, is unfolded, although Fermor and Fox have located gentle warps in the traps of the Linga area (1916, p. 81). There are, however, as already mentioned, parts of the western region where the lavas show distinct dips and folding. The Cutch lavas have been corrugated into anticlines and synclines. In south-east Saurashtra the traps dip about 10° S.S.E. The Rajpipla lavas are described by Blanford as being folded quite strongly, and now possess dips of up to 20° with axes in an E.N.E.-W.S.W. direction. The Panvel flexure is a conspicuous feature running for a known distance of 200 miles north-south from Chiplun to Panvel and the coast west of Daman. Finally may be mentioned the traps at the foot of the south wall of the Narbada rift, which had been dropped down thousands of feet by normal faults and were subsequently folded (Crookshank, 1936, pp. 261, 265, 286). Such folding, implying compression, presumably arose after the tensional stresses had ceased to operate. Some of it may have taken place as late as the Miocene, although there is no direct evidence in favour of this supposition. Moreover, if the descriptions of the Rajpipla area are correct, it is probable that the successive pulsations of tension and compression were not simultaneous throughout the area now occupied by the traps. As will be discussed later, in connection with the Garo-Rajmahal gap, movement may have continued intermittently along the Panvel and other axes into the Pleistocene.

9. *Depression of the Crust during Eruption of the Deccan Traps*

The evidence regarding the manner of eruption of the Deccan Traps, and by inference also of the traps of the Rajmahal Suite, is that the lava flows were not erupted below sea-level. A study of the fauna and flora in the inter-trappean beds has led to the conclusion that the inter-trappeans were deposited under marshy conditions near the mouth of a large river (Hora, 1938, p. 372). This deduction implies that the associated basalts of plateau type were erupted at an elevation which was not much above sea-level. Since the volcanic pile of the Deccan Suite is certainly over 5,000 feet thick where fully developed (and may be even 10,000 feet thick), it is probable therefore that there was a gradual subsidence of the earth's crust *pari passu* with the eruption of successive flows.

This conclusion is suggested also on other grounds. The indications are that the crust was in a state of tension during the eruption of the Deccan Traps. The crust was broken up not only by deep fractures, along pre-existing lines of weakness, such as represented by the Narbada rift, but by other more numerous tensional faults which developed during the course of eruption (Crookshank, 1936, p. 284). Since the crust was under tension, the tendency would be for it to subside differentially into the asthenospheric shell, rather than to rise as might be expected under compression.

The mechanics of crustal deformation are certainly extremely complicated and cannot be explained in any simple manner. Compression in the orogenic belts is thought to be capable of forcing down the light crust into the lower shell as well as raising adjacent parts above their original level. Moreover, both along the Bombay coast and the Narbada zone gravity data suggest that there has been an upwarp of the basaltic shell into the overlying granitic crust. Indeed, this deep-seated upwarp is probably one primary factor in the formation of the weak zone along the Narbada. Consequently, considering only the interface between the crust and the basaltic shell, there has been an elevation of basic material at the expense of the granitic crust along the Narbada zone.

But the general conclusion would seem to be valid that during the period of eruption of the Deccan Traps, involving the up-welling of probably not less than 100,000 cubic miles of basalt magma from the underlying shell through a crust under tension, the tendency would be for subsidence of the granitic crust along normal faults into the underlying shell.[1] Such faulting inevitably involves the formation of an upthrow as well as a downthrow side, but the emphasis is on relative degrees of tilting, subsidence and floundering, rather than on the elevations of the up-throw sides forming significant heights in the zone of the present Satpura trend.

It is necessary, therefore, to picture an irregular pre-trap topography gradually being depressed and flooded with lava flows. It is known that the Deccan Traps of Kathiawar, Bombay and Bhusawal have been subsequently depressed by as much as 1,500 feet (Fermor, 1925, p. 97; Auden, 1949, p. 148). Moreover, Crookshank has shown that the traps on the south side of the Narbada valley have been dropped down by faults by thousands of feet relative to those on the plateau south-east of Pachmarhi (1936, p. 265). Fermor mentions work by Fox which suggests that the fault scarp along the southern side of the Gawilgarh Hills overlooking the Purna trough of Ellichpur has a downthrow of at least 1,800 feet, and possibly as much as 4,000 feet (1930, p. 409). These movements, involving the whole pile of lava flows as now exposed, evidently took place at the end of the Deccan Trap episode, possibly in Oligocene or Miocene times.

10. Post-Tension Elevation

On the other hand, as already stated above, Deccan Traps also occur as outliers at an elevation of over 3,000 feet in Jashpur. This presumably implies a raising of the basement and overyling traps by at least 2,000 or 2,500 feet in the eastern part of the trap outcrop subsequent to eruption. The differential movements between Bombay and Jashpur would amount therefore to not less than 3,500 to 4,000 feet. The distance between the two areas is about 750 miles, so that if there were uniform tilting, the imposed gradient of 1 : 1,000 would be scarcely noticeable.

Now taking the possible north-south component of tilt, the changes in elevation of the trap outliers is from 3,200 feet in Jashpur to 1,600 feet near Ramkola and again 1,600 feet for the titaniferous bauxite (of possible trap origin) on the Rohtas plateau. This northerly tilt between Jashpur and Ramkola is much greater, being 32 feet per mile, or 0° 21′, but would be difficult of observation.

If the lavas are in fact horizontal, the different elevations may be explained either on the supposition that the different outliers do not represent lavas of the same age, or by the existence of block faulting between horizontally disposed traps of the same age. Crookshank has shown that block faulting of post-trap age occurred along the northern edge of the Satpuras near Pachmarhi and that the traps in the Narbada valley were considerably folded. The base of the traps at Pachmarhi is now 3,000 feet, and the uplift relative to sea-level is probably the result of compressional movements which set in after the period of tension. He also points out that the difference in level of traps containing inter-trappeans of approximately the same horizon between Pachmarhi and Nagpur, 100 miles apart, is about 2,000 feet, and suggests that this faulting occurred subsequent to the eruption of the flows (p. 287), though folding and tilting during the post-tension phase may be considered as an alternative explanation. The difference in levels

[1] Normal faults would not persist throughout the whole thickness of the crust, but would be replaced by curved tensional fractures following shear planes in the lower crustal levels (Auden, 1949, 137, 138). In this discussion the emphasis is on the dominance of normal tensional faulting in the upper crust during the period of eruption of the traps in the Peninsula and in the geosynclines of the northern orogen.

due to this tilting would be 20 feet per mile. This angle of 0° 13′ would not be observable at any particular place, and could only be demonstrated by detailed study along the trap outcrop using characteristic flows as datum lines.

The Rajmahal Traps lie close to sea-level, and Blanford and Dunn have concluded that the crust has undergone little change in elevation at the latitude of Rajmahal since the Jurassic period, the crust at this latitude having acted as a hinge zone (Dunn, 1939, p. 142). This matter will be referred to subsequently.

11. Older Alluvium of the Narbada and Tapti

The Narbada and Tapti rifts are of considerable importance to the problem under discussion. The Narbada rift contains fluviatile and probably lacustrine deposits. Representatives of the younger Siwalik rocks are present below the superficial alluvial deposits of the present river (De Terra, 1939, p. 314). Three disconformities, associated with lateritic gravel and soil, are found within an exposed section of 130 feet near Narsinghpur, and a Middle Pleistocene fauna, together with early Palaeolithic tools, occur in the lower group of gravels and concretionary clays. De Terra concludes that the climate had assumed its present dry tropical character at the time of early palaeolithic man (p. 316), but also states that the climate is now drier than it was during the Middle Pleistocene (p. 318). The gasteropods and lamellibranchs found in the Upper Narbada group were all (with one exception) fresh-water forms. Oldham also stated that no marine forms are known (1893, p. 400).

On the other hand, the clays, sands and gravels of the Purna or Purana branch of the Tapti rift along one well-defined zone contain saline water which is extracted from brine wells going down to a depth of 120 ft. The origin of the salt is not known. Common salt is present in contrast to the carbonate, bicarbonate and sulphate efflorescences occurring as *reh* salts in the alluvial plains of the United Provinces and the two Punjabs, and it is possible that the salt is connate sea water that was caught up in the formations at the time of deposition. No marine fossils have been found in these rocks, but Oldham puts forward the very reasonable explanation that during the last Tertiary or early Pleistocene the land was 1,000 feet lower and a branch of the sea may have extended up the Tapti valley to the region of the present Purna river (Oldham, 1893, p. 401). If this explanation is the correct one, and it is difficult to suggest an alternative, it would follow that no major range existed at the end of the Tertiary area in the Tapti area.

It is true that an elevated region is required as a provenance of the rocks of Siwalik type in the Narbada and Tapti. Oldham's explanation was that the land lay to the west, which is difficult to accept as probable if the sea lay in that direction. It might have been the present Satpura range of Pachmarhi, which would imply that the cover of Deccan Traps originally present had been eroded away, with the resultant exposure of the underlying Gondwana sandstones and clays which could have acted as a source for the Narbada sediments. These detrital deposits in the two rifts may thus represent the southernmost extension of the Siwaliks during Pleistocene times. Siwalik rocks occur along the southern foot of the Shillong plateau, and it is not impossible that the Tertiaries of the Chittagong Hill Tracts, Tripura, Sylhet and the south wall of the Khasi and Garo Hills made a sharp deflection and at one time extended in a W.S.W. direction towards Ranchi, Jubbulpore, Seoni and Amraoti, and the Arabian sea.

From two lines of evidence it is suggested that there was uplift near longitude 84°, for the base of the Gondwanas is raised in this region relative to Bengal, whereas the Deccan Traps appear to be similarly raised relative to Bombay. In addition, indications suggest a tilt downwards towards the north. This particular region of postulated uplift is close to the junction of the two downwarps shown in the crustal structure map of India.

In this connection may be mentioned the suggestion put forward 15 years ago by Graaff Hunter that the region of underload in North Bihar has been subject to a secular rise in levels, amounting to a maximum of 0·06 ft. (18 mm.) per annum along a line running between Banaras and Muzaffarpur (1934, p. 236). The existence of this secular rise has been disputed, and it appears still to be undecided to what extent the variation in levels during the course of the last 100 years is due to errors or to a systematic change involving actual secular elevation of the alluvium in the underload area. The line of zero change is shown by Graaff Hunter as passing through Burdwan and heading towards the Mainpat region, where geological evidence indicates the maximum amount of uplift during the late Tertiary and Pleistocene. It is premature at present to do more than point out the interpretation provided, but fuller data are required before the suggested secular rise is substantiated. Graaff Hunter's conclusions are worth bearing in mind in connection with the change in course of the Kosi river during the last 170 years south of its emergence from the Himalaya.

12. *Dunn's Uplifts in Chhota Nagpur*

Dunn has concluded that at the latitude of Rajmahal (25°) the crust has undergone little change in elevation since the Jurassic, and has acted as a hinge zone. North of the hinge there has been progressive downwarping in response to the Miocene and later Himalayan movements, which has allowed the accumulation of over 6,000 feet of fresh-water alluvial sediments in the north Bihar basin. Nearly the whole pile of these sediments now lies below sea-level (Wadia and Auden, 1939, pp. 133–135). South of this hinge line there has been progressive uplift, which has been summarized by Dunn as follows (1939, p. 141):—

(1) Uplift of 1,000 feet of an early Tertiary peneplane, with a downward tilt to the north-east.
(2) Middle or Upper Tertiary uplift of 1,000 feet reaching a maximum in the Ranchi plateau, with a downward tilt to the north-east.
(3) Further uplift of 300 feet.
(4) Final uplift of 400 feet.

The total uplift in the Chhota Nagpur area along latitude 23° was therefore of the order of 2,500 to 2,700 feet, with nil movement along latitude 25°. Since this uplift has taken place during the Tertiary and Pleistocene, it is evident that in early Tertiary times the land was at a lower elevation, and there is not much support for the idea of a major range existing to account for the migration of faunas.

It is true that Parasnath Hill, 4,480 ft., rises above the highest of the Ranchi plateaux, and may represent the residual of a still higher land surface. But even if it is supposed that a total thickness of almost 4,000 feet of rocks have been removed by erosion in the Parasnath area, it is not possible to assume that the original level of the Parasnath plateau was then at the present level of the top of the hill. Other evidence, discussed above, indicates that the total uplift in the Chhota Nagpur plateau was 2,500–2,700 feet. Allowing for the line of nil movement along the hinge line at latitude 25°, the uplift in the Parasnath area should have been about 1,300 feet. That is, the part of the crust now represented by the residual summit of Parasnath was probably in Tertiary times at an elevation of about 3,200 feet. The erosion into residual plateaux, and uplift, were doubtless controlled in the main by the Himalayan movements further north, rather than by simple vertical isostatic adjustment in a crust devoid of compressional restraints.

Crookshank estimates that about 1,350 feet of lavas and underlying Gondwana rocks have been removed by erosion in the central region around Pachmarhi since the last of the flows was erupted (1936, p. 180). The highest peak of the Satpuras at Pachmarhi is Dhupgarh 4,429′. In this case also it would be most unwise to assume that the original height of the region was $4{,}429' + 1{,}350' = 5{,}779'$, because uplift has certainly taken place concomitantly with erosion.

III. The Garo-Rajmahal Gap

1. *Position of Possible Connection*

The nature and age of the Garo-Rajmahal gap received considerable discussion after the reading of Dr. Hora's paper on 'the Malayan Affinities of the Fresh-Water Fish Fauna of Peninsular India' (1944, pp. 434–439). A. N. Thomas in the first place considered that the real connection between the Rajmahal area and north-east India lay not in the present Garo-Rajmahal gap, but between Monghyr and the Darjeeling-Nepal Himalaya. This hypothesis would appear to be untenable for the following reasons:—

(1) The north-south strike of the Archaean rocks at Monghyr is almost certainly only a local deflection of the general E.N.E.-W.S.W. strike of the northern edge of the peninsula between Gaya and Rajmahal. The regional direction of strike is in fact that of the inliers sticking up through the alluvium along the line Gaya-Sheikhpura-Lakhi Sarai, and at Banka, 20 miles south of Bhagalpur. The strongly compressed folds in the hill mass south of Monghyr, and 12 miles W.S.W. of Bhagalpur, appear to represent no more than acute-angle flexures of local extent. The archaean strikes thus favour the supposition that the connection lay, where it has generally been supposed, between the Garo Hills and the Rajmahal area.

(2) The Gangetic downwarp of North Bihar, characterized by strongly negative gravity anomalies, extends in a W.N.W.-E.S.E. direction as far east as Purnea, almost orthogonal to the connecting range postulated by Thomas. This would be an unlikely disposition since the downwarp, and infilling with a great thickness of alluvial sediments in the form of an orogenic trough, cut right across the supposed connection.

(3) Evans and Crompton have shown that a zone of positive H-anomalies of more than 25 milligals extends for 140 miles in an almost N.E.-S.W. direction from Suri to Dinajpur, accompanied to the south-east by a parallel zone of weaker negative anomalies between Burdwan and Bogra. These zones are suggestive of sub-crustal warps in the general Garo-Rajmahal direction, and lend support to the idea that the original connection lay in the present gap (1947, p. 233).

Both surface strikes in the Archaeans, and the sub-crustal warps indicate, therefore, that the probable connection lay in a N.E.-S.W. direction between Malda and Dhubri, and not between Monghyr and the Darjeeling-Nepal Himalaya as supposed by Thomas.

2. *Age of Connection and Formation of Gap*

Little agreement exists about the age of the Garo-Rajmahal gap. Thomas considered that it is an old and persistent feature which has been of low level continuously from late Cretaceous or early Eocene times. Krishnan and Aiyengar favoured a mid-Miocene age for the gap, remarking that no convincing tectonic cause was available at a later age to explain the formation of the gap (1940, p. 9). That assumption is, however, untrue, because the Siwaliks have been compressed, folded and thrust into well-defined blocks during the later Pliocene and Pleistocene. Major late-Tertiary thrusts are known, for example, in the Siwaliks of eastern Nepal, having been noticed south of Katmandu and Udaipur Garhi (Auden, 1935, p. 144) and having been mapped in detail in the Jhapa area by E. Lehner (unpublished report).

Moreover, such folding is known also to have occurred in the peninsula area. Reference has already been made to the unconformity which exists between the

Laki (Middle Eocene) or pre-Laki lateritic group and the underlying Deccan Traps, Cretaceous and Jurassic rocks of Cutch, which signifies gentle movements and erosion. Subsequently, the middle Tertiary and earlier formations of Cutch were strongly folded into sharp anticlines and synclines, between latitudes 23° and 24°, the northernmost folds of Patchham, Khadir and Bela islands probably occurring in échelon formation against the rigid pre-Cambrian shield of which Nagar Pakar (24° 21′ : 70° 43′) is a conspicuous remnant (Wynne, 1872, pp. 110, 133, 145, 146, 201, 202). This major folding may have occurred during the same Miocene period as the maximum thrust movements of the Himalaya and the uplift of the Shillong plateau. Finally, unconformable relations were involved between the Upper Tertiaries of Cutch and the underlying Miocene, Eocene, Cretaceous and Jurassic rocks. In the Cutch region there were therefore three periods of folding:—

(1) Mild folding in Ranikot (Lower Eocene) times, after eruption of the Cutch traps, with extensive unconformity of the Lower Eocene laterite group across traps and Upper Jurassics.
(2) Strong folding and faulting in post-nummulitic times; probably Miocene.
(3) Moderate folding and faulting in Pliocene or Pleistocene times, involving the whole sequence.

Consequently, both on the north and west sides of the Peninsula there were repeated movements, while in the orogenic downwarp south of the Himalayan Siwaliks movements of a pronounced nature have persisted into post-Siwalik times. Indeed, it may not be straining comparisons too far to relate the pre-Cambrian shield of Rajputana with the wedge of ancient rocks now represented in the Khasi and Garo Hills (Figure 2), and to consider the folds at the east and west extremities of India connected with these wedges as homologous.

It is desirable to extend the discussion of the earth movements which involved the outer Himalaya north of the Garo-Rajmahal gap. Heim has emphasized the forward sweep of the Daling metamorphics which truncate the strike of the Siwaliks to the east of the Darjeeling foothills, particularly between the Kalijhora and Torsa rivers (1938, p. 419). The interpretation put forward by Heim is that the Daling metamorphics were pushed 20 km. (12½ miles) over an eroded surface of the Siwaliks. I do not know the area concerned, but the available evidence in other parts of the Himalaya is that the Daling and equivalent thrusts are of Miocene age, and did not involve translation over the younger Pliocene-Pleistocene Siwalik rocks. An alternative explanation is that the Daling rocks were thrust upon Gondwanas during the Miocene, and that the whole block of Daling and underlying younger Gondwanas was brought forward against the Siwaliks by strong tear faults during the Pleistocene.[1] Whichever explanation is correct, it is certain that late movements of considerable intensity must be accepted and the validity of the argument put forward by Krishnan and Aiyengar is doubtful.

Fox shows that the present area of the Garo and Khasi Hills was under sea until the end of the Mesozoic, and that the sea fell back from the Khasi Hills during the Upper Eocene and from the Garo Hills during the Miocene. The Shillong plateau came properly into existence in the Miocene, at which time Fox considers that the structural sag of the Garo-Rajmahal gap also formed, the implication being that there never was a pronounced topographical expression between the Garo and Rajmahal hills (Fox, 1944, p. 437). South of the Khasi Hills there is a pronounced downwarp, filled with Upper and Lower Tertiary sediments and overlain by alluvium. Evans and Crompton show that the geological correction required for the gravity data amounts in the Sylhet area to over 75 milligals, with a positive sign due to the

[1] Late Pleistocene tear faults are found in the gaps cut by the Ganga and Yamuna Rivers through the outer Siwalik Range, and these lines of weakness were evidently responsible for the courses adopted by the two rivers.

existence of low-density sediments (1947, p. 221). Moreover, the shape of the 75 milligal isogam correction suggests that these Tertiary rocks were folded along north-south axes, in strike continuation with the folds of Tripura and the Chittagong Hill Tracts (1947, p. 228). Since the folding involves also the Upper Tertiary rocks, it is clear that movements subsequent to the elevation of the Shillong plateau took place in the region.

It is not impossible, therefore, that the Miocene uprise of the Shillong plateau also witnessed a similar uprise and connection in the present Garo-Rajmahal gap, and that the gap was breached at a later date, at the same time as the Upper Tertiary rocks of Sylhet, Tripura, and Chittagong were folded along axes with north-south strikes and the last folding and faulting in the Cutch area took place. This late dating of the formation of the gap was the view maintained by Pascoe (1919).

This connection must have had a N.E.-S.W. strike extending from Dhubri to Malda, because the Garo and Khasi Hills lie north of the latitude of the Rajmahal hinge line of zero movement, and more or less on the same strike as the zone of maximum downwarp 200 miles to the west in North Bihar. Indeed, the region of the gap, now covered by alluvium, must clearly be one of great structural complexity, involving sharp changes in strike and abrupt terminations of structures.

In this problem the excellent paper by Evans and Crompton on geological factors in gravity determination is of great value (1946). In figure 4, page 221, these authors have worked out the geological corrections which should be applied to the gravity data in Burma and north-east India, based on extensive geological and geophysical studies. A striking angular insertion of an area of moderate geological correction (+25 to 50 milligals) is noticed in a region of large correction (+50 to 75 mgl.) near Comilla. If the straight western contour between the 25–50 and 50–75 mgl. correction isogams is extended to the north-west, it strikes the edge of an area of very high correction (greater than 75 mgl.) where the isogam contours are steep, and passes in a short distance to a region of negligible correction. These contours indicate the effects of rapidly varying depths of low-density sediments of Tertiary and post-Tertiary age lying within the topmost 40,000 feet of the earth's crust.

Figure 12 of their paper (page 233) shows the gravity anomalies after full correction has been made for surface geological formations and isostatic compensation. It is seen that a zone of low negative anomalies running between Burdwan and Bogra terminates abruptly against a region of high positive anomalies related to the Shillong plateau. Indeed, there is a narrow gap of zero anomaly just west of the Garo Hills which separates anomaly isogams both of different sign and different geographical alignment. There is reason to believe, therefore, that the sharp discontinuity seen on the surface is also reflected not only in the distribution of masses of Tertiary and post-Tertiary sediments of greatly contrasted thickness, but in the deeper crustal structure as well. All these facts point to some form of crustal discontinuity striking in a N.W.-S.E. direction.

It appears to be more than a coincidence that this N.W.-S.E. line, if continued in a north-west direction, connects up with that of the maximum forward translation of Daling rocks described by Heim near Lat. 27° N., Long 89° E., while in a south-east direction the line follows the coast between Chittagong and Cox's Bazar. The suggestion put forward is that this N.W.-S.E. zone between the Baxa foothills, the western edge of the Garo Hills, Comilla and the Chittagong coast represents a direction along which sag faulting, perhaps accompanied by tear movements with a strong horizontal component, took place in the late Tertiary or Pleistocene, thereby fracturing and breaching the former ridge between the Peninsula and the Shillong plateau which may have been elevated during the Miocene.

This depression may be compared with those of the Gulfs of Cambay and Cutch in western India, where the Deccan Traps and younger rocks have been folded

below sea-level and covered by alluvium. Deep wells indicate that the alluvium between Ahmedabad and Mehsana is over 1,000 feet thick.

Whether or not the depression of the Gulf of Cambay is related to the Panvel flexure is difficult to determine on existing evidence. It is considered possible that the main faulting and folding of the Deccan Traps occurred between the Eocene and Miocene. Since the depression of the two gulfs involves the folding of the Upper Tertiaries, and infilling with alluvium, the final expression of movement must be of very recent date, and the coincidence between the Gulf of Cambay depression and the Panvel flexure may be an example of the rejuvenation of movements along a previously defined direction of flexure and weakness.

A similar rejuvenation of movement doubtless occurred also along the Narbada direction, which is probably an ancient line of weakness, first developed possibly in pre-Cambrian times, and later followed by the Rajpipla folding, dyke clusters and swarms, downfaulting and the infilling of the Narbada rift. The E.N.E.-W.S.W. direction of the Narbada rift, and the E.N.E.-W.S.W. and E.S.E.-W.N.W. directions noticed in the Tapti depressions (the latter direction being perhaps connected with the Cutch folding), suggest the existence of recent movements. The presence of saline beds in the Purna branch of the Tapti catchment has already been stressed, and it is possible that a narrow gulf of sea extended over a downfaulted region of the Deccan Traps as far as Amraoti in the late Tertiary. The diastrophic history of the region is shown in diagrammatic form in Table 2.

IV. Conclusions

1. *Regarding the Ur-Satpura Range*

The geological history of the region extending from the present Satpura range eastwards to the Mahadeo Hills, the Mainpat, Chhota Nagpur, Rajmahal and the Shillong plateau has been examined in the light of the earth movements which affected the Peninsula during the Tertiary and post-Tertiary eras.

Notwithstanding the uncertainty regarding the range of time involved in the eruption of the Deccan Traps, this formation is considered to be a vital one in interpreting the palaeo-physiography of the area. It is clear that eruption of basic lavas in India was a prolonged phenomenon. It began, and was presumably completed, in Lower-Middle Jurassic times in the Rajmahal area. In Sind, Cutch, Gujerat, and probably also Saurashtra, 1,500 to 3,000 feet of lavas were erupted between the Upper Cretaceous and lowermost Eocene, being subsequently exposed to prolonged exposure, and the chemical effects of lateritisation, before the deposition of Laki beds. But eruption over most parts of the peninsula proper is considered to have taken place mainly during the Tertiary era. The sequence of events may be compared in length of duration, therefore, with that which occurred in the north-western Himalaya, where the eruption of the Panjal Traps lasted throughout the Permo-Carboniferous and Triassic.

While in western India the traps lie with very little unconformity upon the older rocks, in the peninsula proper the unconformity upon folded and eroded Vindhyans and Gondwanas is profound. The major compressional movements reacting on the Gondwana rocks were finished, and erosion had occurred, before the deposition of the infra-trappeans or Lametas, of Upper Cretaceous age. This inference also applies to areas where the Lameta beds are missing and the age of the overlying traps is uncertain, but probably Lower Tertiary. The first folding of the Cutch and Gujerat Traps, accompanied by swarms and clusters of basic dykes, took place either at the close of the Cretaceous or in the Ranikot (Lower Eocene). These compressional movements may also have affected the rest of the peninsula, and intensified the folding of the already folded and downfaulted Gondwanas, but the

Deccan Traps of this area show no sign of them, evidently because they were erupted at a later date.

Accepting on palaeontological grounds an Eocene age for the inter-trappeans over most of the mainland, and a similar age therefore for the associated traps, it follows that the physical conditions favouring eruption of the lavas reached fullest development in the central part of the mainland later than in the bordering Rajmahal, Cutch and Gujerat areas. A condition of tension must have set in after the Mesozoic compression, which first possibly finalized the formation of the Gondwana rifts and then, with closer spacing of fractures, permitted the widespread eruption of lavas upon a crust undergoing progressive subsidence. Basic lavas of Cretaceous-Eocene age, associated with peridotites, occur in the montane zone of Sind, Baluchistan, Nanga Parbat and along the Indus river in Ladak. These rocks were intruded and extruded during a phase of tension when the crustal base of the Himalayan and related geosynclines underwent maximum stretch (Fig. 1). This condition of tension is regarded as a vital consideration in studying the Ur-Satpura problem, for it indicates that no elevated range or plateau could have existed in the present Satpura trend during the Lower Tertiary. If Hora's view of a late-Tertiary age of peninsular traps is accepted, then the period of crustal tension and subsidence must have continued into more recent times.

The second period of folding, accompanied by elevation, which took place after the formation of the Narbada rift, may have been of Miocene age, and contemporaneous with the main period of Himalayan overthrusting. The effects of this compressional phase were clearly confined to localized zones, because the greater part of the Deccan and Rajmahal Traps is unfolded. The rise of the Satpura zone south of the Narbada must certainly have created an elevated plateau, with a cover of unfolded traps, but this plateau was involved in rapid erosion, with the concomitant infilling of the Narbada and Tapti rifts by materials removed from the heights, and there is nothing to indicate that the top of the pre-erosion plateau ever existed at a much greater elevation than now shown by its dissected remnants.

The Narbada rift is regarded as a major crustal feature of ancient origin, reflecting sub-crustal structure, and influencing the deposition and folding of the Vindhyans and Gondwanas. It was subsequently a zone of pronounced volcanic and plutonic activity, the three plutonic centres of Kathiawar lying in a curved zone which is a prolongation of the Narbada fracture (Auden, 1949, p. 128, Plate 11).

In the eastern part of the peninsula the hypothetical Ur-Satpura range runs obliquely across the Archaean and Gondwana grain of the country.

The Deccan Traps are not normally covered by younger formations in the mainland. If such formations were ever deposited on the traps, they have since been eroded away and we have no knowledge of their former possible thickness. It is only in the downfaulted or sagged zones of the Narbada and Tapti rifts that younger formations are present.

The existence of saline beds in the Purna branch of the Tapti rift suggests that at the end of the Tertiary this particular area may have been at sea-level. Oldham's tentative explanation was that the Purna area of the Tapti was subsequently raised 1,000 feet, during the Pleistocene. Presumably the contiguous traps were elevated concomitantly. This uplift of 1,000 feet may possibly be contemporaneous with the final uplift of 700 feet deduced by Dunn in the Chhota Nagpur area. The indications are, therefore, that the region cannot have been very high during the late Tertiary.

Maximum elevation of the base of the Gondwanas relative to the eastern outcrops, and of the Deccan Traps relative to the west, appears to have occurred in the neighbourhood of Lat. 23° N.: Long. 84° E. and to have diminished northwards to zero movement at Latitude 25° in the neighbourhood of the Rajmahal Hills.

Dunn postulates that no movement has occurred in that area since the Jurassic period.

It may be remarked that a somewhat analogous disposition is represented in the Himalayan region. The western Himalaya shows the presence of extensive outcrops of para-autochthonous units in windows below the overthrust schistose rocks (West, 1938, p. 133; Auden, 1948, p. 77). In the eastern part of the Nepal-Himalaya, and in Darjeeling-Sikkim, such windows appear to be rare and much more circumscribed. Structural equivalents of the Garhwal and Shali windows do occur in a relatively small semi-window in the Kosi-Tamur valley (Auden, 1946, p. 346) and, from recent work by Ray, probably appear even north of Darjeeling near Nayar Bazar, but they are much less pronounced than in the west. This disposition suggests that there may be a tectonic culmination in the west exposing the lowest structural units, whereas in the east these units are more depressed and lie mostly concealed below the limit of erosion (Auden, 1935, p. 165). In point of view of longitudes, there is no correlation between the elevation of the Gondwanas and Deccan Traps referred to in the preceding paragraph and the western culmination in the Himalaya, but the two phenomena are probably interconnected.

Erosion has certainly been pronounced in the Pachmarhi and Chhota Nagpur regions and numerous residual plateaux have been left. But the crust has been uplifted *pari passu* with erosion, and the original level of the highest plateau was probably little higher than the present summits, even allowing for the subtraction of eroded material no longer observable above the residuals which now survive.

The evidence is not in favour, therefore, of the conception of a major Ur-Satpura range extending across India during the Tertiary period that has subsequently been worn down to the present elevations. It suggests rather the downfaulting along the Narbada and Tapti rifts at the close of the eruption of the traps, and the unequal elevation of the region since the Miocene.

It is considered probable that a connection did arise between the Shillong plateau and the peninsula during the Miocene and that the final break causing the present Garo-Rajmahal gap took place during the Pleistocene along a N.W.-S.E. line of fracture extending from the Darjeeling-Himalaya to Comilla and Chittagong. Consequently, it is necessary to suppose that while the central part of the peninsula was undergoing mild uplift during the Pleistocene, the bordering areas of Cutch, Saurashtra, and northern Bengal were subjected to depression.

2. *The Pleistocene Ice Age and Climatic Conditions*

If, as is suggested from the above discussion, no major range existed during the Tertiary and Pleistocene along the present Satpura trend, which could account for increased precipitation and humidity, and permit the migration of faunas, some other explanation must be adduced to provide for these ecological requirements. It would appear that the solution is to be found in the Pleistocene Ice Age in India, one that was advocated in the first place by the early pioneers of Indian geology. The question of the Ice Age in India has recently received extensive discussion by H. de Terra and T. T. Paterson. These authors (1939, p. 224) correlate the first glaciation with the Tatrot stage of the Siwaliks (Lower Pleistocene), the first interglacial period with the Pinjor stage and the Second Glaciation with the Boulder Conglomerate stage (Middle Pleistocene). Moreover, Morris (1938, p. 414) has described a glacial boulder bed 6,000 feet below the top of the Siwalik succession at Bain (32° 28′ : 70° 33′). This succession is now folded so that, before removal by erosion of the crest of the Marwat Kundi anticline, the Bain boulder bed would have been at an elevation of about 3,700 feet at the crest, and is now well below sea-level at the flanks. Before folding the disposition of the Bain boulder bed would have been relatively flat, but at a height above sea-level which is impossible now to assess on account of regional changes in elevation which have taken place subse-

quently to folding. This Bain boulder bed is correlated with the First Glacial Period of Tatrot age, and indicates the widespread occurrence of glacial conditions in the Siwaliks at *what are now low elevations*, a considerable distance from the main montane zone.

Paterson has shown that the glaciers of the Kashmir valley descended to the present elevation of 5,500 feet during the first and second glaciations (1939, p. 79). In the central and eastern Himalaya there are definite signs of glaciation down to present-day elevations of 7,000 to 8,500 feet. But these elevations were clearly not those that obtained during the Ice Age, because the Himalaya are known to have risen very considerably in late Pleistocene and recent times. The tilting of the Karewas in Kashmir shows vividly how strong and recent these elevations have been.

Finally, the existence of the erratic blocks in the north-western part of the West Punjab, north and south of the Kala Chitta Range, may be mentioned. The origin of these blocks has been the subject of some discussion, which was summarized by Cotter in 1929. Cotter's view is that these erratic blocks may have been left in their present position by large scale mud-flows arising in Hazara, at a time when the climate was colder and the glaciers had a wider extension. He concluded that (p. 334):—

> '. . . . profound changes have taken place in this region of the Northern Punjab since Pleistocene times, and it does not seem impossible that at a former period natural forces were on a sufficiently grand scale to bring about such catastrophic glacial outbursts of water or of mud-avalanches as might have brought the erratic blocks of Attock District to their present position.'

It is likely that the land in Northern India may have been from 1,000 to 3,000 feet lower in the early Pleistocene than it now is, and that the glaciers must have descended to levels which were then that much nearer sea-level. While the present glaciers of the Karakoram and Himalaya, great though some of them are, have little effect on the climate of the Peninsula, it is almost certain that with a snow line and glacier line possibly 6,000 to 8,000 feet lower than now obtains (allowing for glacier recession as well as isostatic rise) the temperature and humidity conditions in northern India must have been markedly different. The temperature would be lower, and the relative humidity greater. It is considered probable, therefore, that it is these climatic factors, associated with a lower elevation of the Himalaya mountains, which permitted migration of faunas rather than the existence of any pronounced elevation along the present Satpura trend.

3. *Evaporation Losses and Run-off*

Engineers have long been concerned with the calculation of run-offs from catchments in connection with estimates for reservoir storage. Barrows (1943, p. 117) has quoted a formula developed by Vermeule for river basins in the north-eastern part of the U.S.A.:

$$E = (11 + 0{\cdot}29\,R)\,M$$

in which—

E = annual evaporation or water losses, in inches.
R = precipitation, in inches.
M = factor depending on the mean air temperature, varying from 0·77 for 40° F. to 1·47 for 60° F.

Other formulae include factors such as slope and degree of vegetal cover. Recently A. N. Khosla (1949), following the same lines as Vermeule, has introduced a new formula in which all losses, whether by evaporation, transpiration, or

percolation into the ground, are regarded entirely as a function of temperature. His formula is:

$$L_m = \frac{T_m - 32}{9 \cdot 5}$$

L_m = monthly losses due to all causes, in inches.

T_m = mean monthly temperature in degrees Fahrenheit.

By subtracting the monthly losses from the monthly precipitation and summing for the whole year he arrives at a figure for the annual run-off. For a given precipitation, therefore, the losses are higher and the run-off is consequently smaller in proportion to the increase in temperature. This is of course to be expected, but the close correspondence between calculated run-offs, on the assumption that temperature is a complete measure of all the various factors which are responsible for the loss of rainfall to run-off, and the actual run-offs is certainly surprising.[1] A comparison is given in Table 3 between catchments with more or less similar precipitations but widely different mean annual temperatures, the figures being selected from Khosla's paper.

TABLE 3

	Precipitation in inches	Annual mean temp. °F.	Inches		
			Calculated loss	Calculated run-off	Actual run-off
Mahanadi	56·68	80·07	29·31	27·37	28·33
Ashni, Simla Hills	57·20	58·10	22·93	34·27	35·80
Difference	0·52	21·97	6·38	6·90	7·47
Indian rivers flowing into Arabian Sea	47·00	70·0	23·7	23·3	..
Brahmaputra system	48·11	46·8	18·47	29·64	..
Difference	1·11	23·2	5·23	6·34	..
Cauvery, India	38·91	72·7	34·13	4·78	..
Merrimack, U.S.A.	41·63	45·6	21·50	20·13	..
Difference	2·72	27·1	12·63	15·35	..

These figures show that, for a difference of 20°–30°F. in the mean annual temperature, the run-offs for these particular catchments with closely similar rainfalls differ in magnitude by 6 to 15 inches. This affords an indication of the increase in run-off which might be expected in India during the Pleistocene, when temperatures were lower. The monthly temperature variations were also probably smaller, which would tend, with a lower mean annual temperature, to equalize evaporation losses, and cause both a more uniform monthly discharge and a greater total annual discharge. The land elevations were, of course, different during the Pleistocene, being without question lower over most of the montane zone in the north. But the influence of lower elevations in decreasing precipitation was probably less than the effect of a lower mean annual temperature on relative humidities and evaporation losses to the precipitation, and it may be assumed that the net effect was that the run-offs and river discharges were higher than at the present day. The emphasis would be therefore not so much on the physiographic conditions necessary to cause

[1] That exceptions to this generalization exist may be seen, however, in comparing the Damodar and Chattahoochee Basins, and the Sabarmati and Mississippi basins.

increased precipitation, but on the factors responsible for reduced losses to the precipitation, which need not have been very different from what it is at the present day.

The primary factors involved in this problem of faunal migration would appear, therefore, to be the following:—

(1) A secular climatic change, involving 4 or 5 glaciations, with interglacial periods which were probably cooler than any climate experienced now in central and southern India.

(2) The glaciers during the periods of ice advance reached much lower down the valleys, and glacial boulder beds have been found recently even to be incorporated within the Siwalik succession of northern India.

(3) Not only did the glaciers reach to lower levels as a consequence of a colder climate, but during the Pleistocene the montane zone must itself have been at smaller elevations. The influence of the glaciation on the climate of the Peninsula must therefore be considered from the dual point of view of an intrinsically colder climate in the mountains and the existence of glaciers at lesser elevations than even the present heights of maximum ice advance indicate. During the phases of maximum glacier advance the snouts of the glaciers may have been, from combined climatic and isostatic causes, some 6,000 to 8,000 feet lower than at the present time.

(4) It is difficult to avoid the conclusion that these conditions in the montane and bordering zones of northern India must have resulted in a diminution of the temperature in the region now represented by the Satpura and Vindhyan ranges. A lowering of the mean annual temperature in these regions of only 20° to 30°F., which would still be considerably above the freezing temperatures of the glaciated region to the north, would permit much greater run-off and larger river discharges for an equivalent rainfall.

(5) The greater relative humidity and higher river discharges would perhaps be sufficient explanation for the migration of the faunas postulated.

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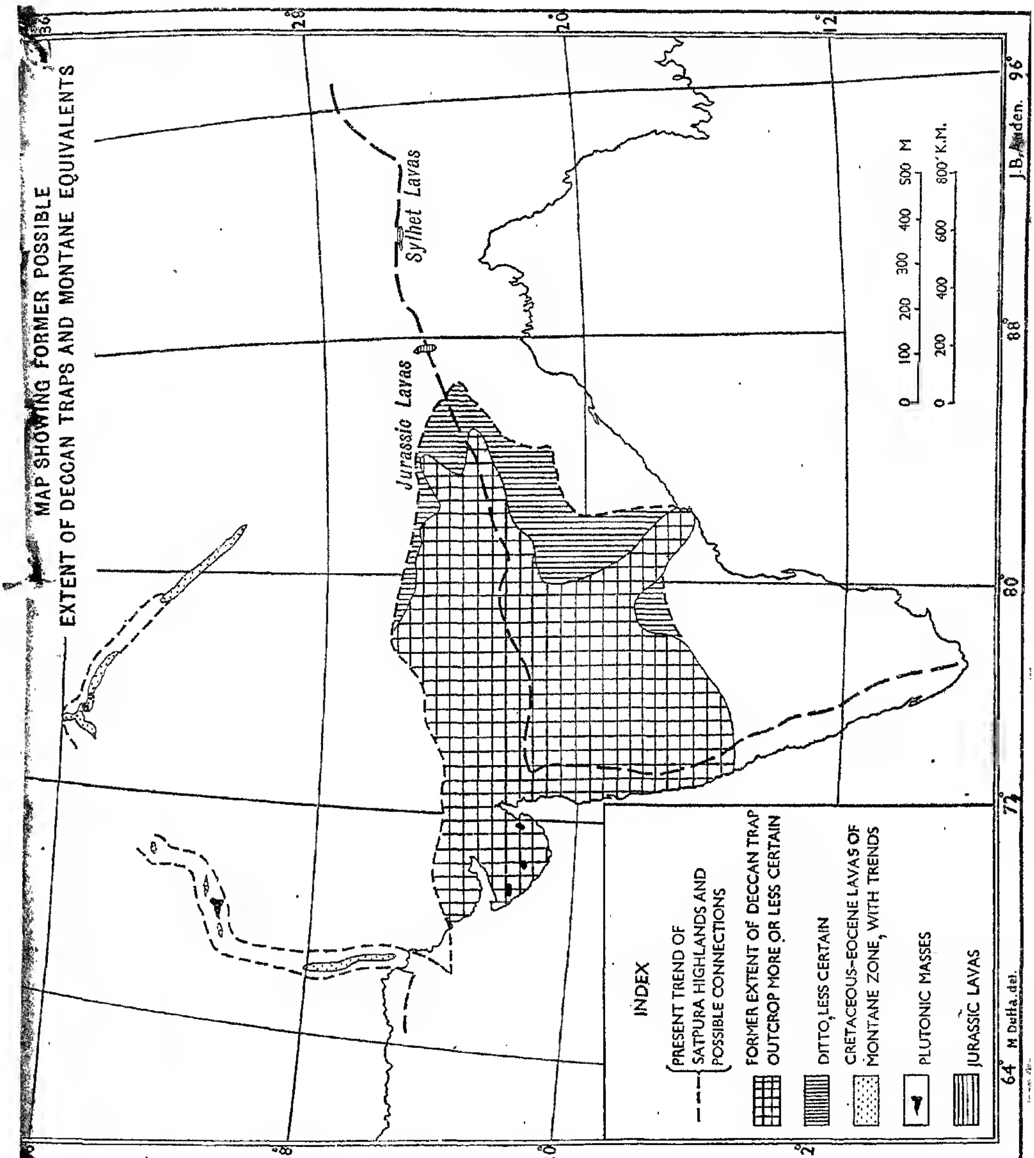
MAP SHOWING FORMER POSSIBLE
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DITTO, LESS CERTAIN
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PLUTONIC MASSES
JURASSIC LAVAS
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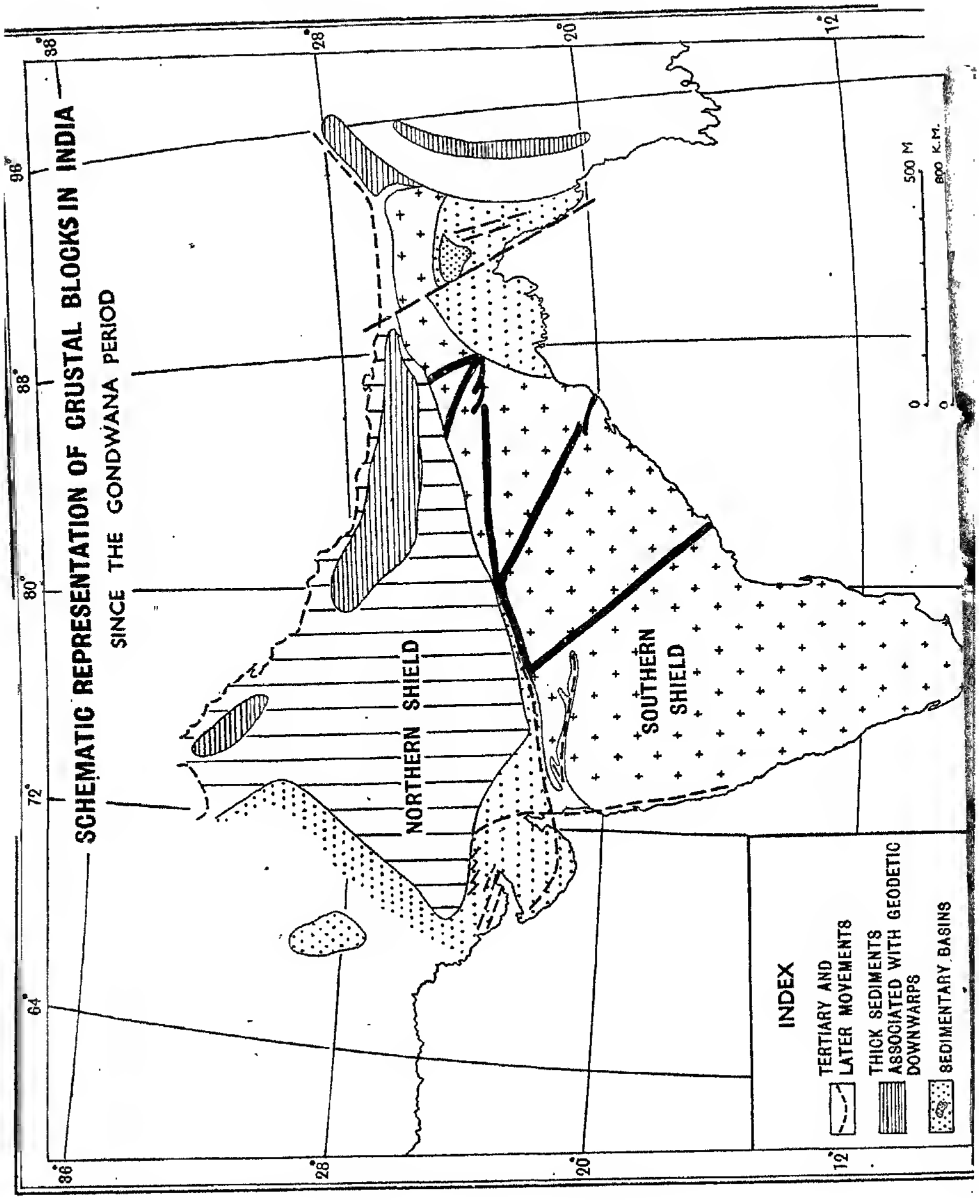
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NORTHERN SHIELD
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INDEX
TERTIARY AND LATER MOVEMENTS
THICK SEDIMENTS ASSOCIATED WITH GEODETIC DOWNWARPS
SEDIMENTARY BASINS
0
500 M
0
800 K.M.
36°
28°
20°
12°
38°
64°
72°
80°
88°
96°

LAND CONNECTIONS BETWEEN CEYLON AND PENINSULAR INDIA.*

By K. JACOB, *D.Sc., F.G.S., F.N.I., Geological Survey of India, Calcutta.*

Ceylon remained geographically a part of the Indian mainland until quite recent times. The island was first severed during the Miocene epoch when a wide arm of the Tertiary sea extended across the southern parts of the peninsula. This phase in the geological history of the island is indicated by the marine fossiliferous deposits laid down in the northern and north-western parts of Ceylon extending from Puttalam on the west coast to Mullaitivu on the east including the whole of the Jaffna peninsula in the north. The Puttalam Jaffna sediments, according to Davis (Wayland and Davis, 1923), may be as late as Pontian or Sahelian (Lower Pliocene) which, geochronologically stated, may probably be as old as fifteen million years. Similar, more or less contemporaneous, depression of land in the neighbouring parts of southern India is suggested by the very closely related Quilon beds of Travancore on the west coast.

This state of severance in the early history of Ceylon did not last long. Connection with the mainland was again established as the result of a slow uplift since the close of the Miocene-Lower Pliocene times which brought most of the sediments above the level of the sea. There were later minor oscillations of the level of the land and sea of sufficient magnitude to disturb the migratory land routes between the Indian mainland and Ceylon. Interchange of plants and animals took place whenever land connections were established and suitable climatic conditions prevailed. This is evidenced by the existence of closely related Himalayan fauna sustained on the mountains of Ceylon, and identical South Indian fauna thriving in the drier zones of the plain. It is surmised that the hill fauna entered during a 'cool, pluvial spell' and the other at a time when arid conditions prevailed (Deraniyagala, 1944). 'The failure of the former animals to withdraw to the Himalayas when arid conditions commenced, suggests that Ceylon had by then become isolated so that the entry of the latter group could only have occurred during a subsequent reconnection with the mainland' (Deraniyagala, 1944).

Further evidence of recent subsidence and emergence that might have effected land connections with the peninsula are not entirely wanting. The presence of the pearl oyster on the coastal 'pseudo-cliffs' would indicate former emergence while the sunken valleys of rivers, particularly of the Marichhukata which in earlier times probably extended beyond the present Vangalai pearl bank to the north-west of Ceylon, would point to earlier subsidence (Deraniyagala, 1946). It appears likely that this disruption of land area which probably lay in the route of migration occurred in post-Pleistocene times.

The recent discovery of vertebrate remains in the Ratnapura beds of Ceylon throws fresh light on the post-Pliocene phases in the migration of land animals into Ceylon. It would appear on the evidence of the Ratnapura fossils, that land connection between Ceylon and the mainland was in existence even as late as Upper Pleistocene, approximately, 25,000 years ago.

From a detailed study of several Siwalik forms Deraniyagala (1944) concludes that the Ratnapura fossiliferous horizon ranges in age from the Pinjor † to relatively

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† *Recent.*

U. Pleistocene	Kurnool
M. Pleistocene	Narbada
L. Pleistocene	Boulder Conglomerate Pinjor
U. Pliocene	Tatrot Dhok Pathan.

recent (post-Kurnool) times. The association of *Merycopotamus*, *Hexaprotodon* and *Elephas maximus* in the same beds is of particular interest. In the Siwaliks, *Merycopotamus* first appears in the Dhok Pathan stage or earlier, and extends to the Upper Pinjor, while *Hexaprotodon* manifests itself in the Tatrot and continues to persist into the Boulder Conglomerate of the Siwaliks and the later Narbada and Godavari deposits. In the Ratnapura beds the occurrence of the remains of an extinct race of the recent *Elephas maximus* along with the above two older forms may appear perplexing. Deraniyagala (1942), however, suggests that these beds contain both an older as well as a relatively recent fauna, re-assorted and re-deposited, and ranging in age from the Pinjor to post-Kurnool. Although *Merycopotamus* and *Hexaprotodon* might have migrated to Ceylon during the Upper Pliocene-Pleistocene times, *Elephas maximus* could have done so only at a much later date, very probably after the Upper Pleistocene when a land route was still operative. It would appear, therefore, that the final disruption of the island as a separate geographic entity did not take place until after the Upper Pleistocene.

Further direct geological data seem to be lacking. A study of the earth movements of the Ceylon-South Indian region accords indirect support to the views expressed above. It is not unlikely, as pointed out by Wadia (1941, 1943 and 1943*a*) that, of the two major uplifts in Ceylon, the last involving the highest, but topographically 'immature' terrain of the island, was more or less contemporaneous with the Nilgiri-Palni upwarp, the scarp faulting on the West Coast and the Narbada-Tapti system of faulting. How far these cataclysmic changes, believed to have taken place as late as Pliocene (? or even later), directly affected the relationship between Ceylon and the Indian peninsula since Miocene times, is not known with any degree of certainty. But it is likely that these movements might have influenced the regions profoundly re-establishing the land connection during the Pliocene (Wadia, 1943*a*) * and thus enabling the Siwalik animals to migrate to Ceylon. In this connection it is of some significance that the earliest record of the Siwalik fauna in Ceylon occurs in the Ratnapura beds which are not older than the Upper Pliocene. The 'evidence', though indirect, is worth further consideration.

Recent archaeological discoveries offer some fresh evidence on the separation of Ceylon (probably the final disruption of the land link with the Peninsula) in comparatively recent times. The old stone age Ratnapura man of Ceylon shows hardly any signs of progress in his industries as compared to those of the palaeolithic man of Madras, probably owing to his isolation on an island. It is quite possible, as Deraniyagala (1946) suggests that they were 'suddenly exterminated when a new land bridge enabled the neolithic Balangoda man to enter from India'. If this hypothesis is acceptable, connection with the mainland was in existence intermittently as late as, or even later than 10,000 years ago.

Arldt (1919) who made extensive palaeogeographical studies, also concludes that Ceylon finally became separated from the mainland during the Quaternary. His observations are mainly based on zoogeographical considerations. Arldt's map (1919) of the world during the Quaternary epoch (including Pleistocene) represents Ceylon as a continuous extension of the mainland. Seward (1933) is in agreement with Arldt in depicting Ceylon as a part of peninsular India in his palaeogeographic map of the early Quaternary.

A few points are, however, raised by Deraniyagala (1943) which tend to throw some doubt on the probable routes of migration of the Siwalik and recent fauna into Ceylon by way of southern India. 'The absence from Ceylon of many extinct animals common in other Siwalik areas, the presence of the hippopotamus which is unknown in South India, and the existence of a strong Malayan element in Ceylon's living faunas, suggest the not impossible view that its Siwalik fauna

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* Wadia (1943*a*, p. 19) expresses the opinion, based on other evidence, that the connection with the mainland was restored for the most part by the middle of the Pliocene.

did not enter direct via South India.' But it is pointed out by Deraniyagala (1946) in a later paper, 'Since the bulk of Ceylon's extinct and existing species are barely separable from their Indian counterparts, their main route of entry was apparently longitudinally via India, but the fact that Ceylon also possesses African and Malayan faunistic elements unknown from India suggests supplementary temporary connections . . .' In the paper quoted above the author gives specific instances of related African and Malayan elements in the Ceylon fauna. It seems, however, doubtful if the Malayan element spread to Ceylon by way of temporary island connections as suggested by Deraniyagala. Possibly it reached Ceylon by way of the predominantly humid regions of the Indian mainland which afforded satisfactory conditions for migration during geologically recent times. Hora's (1949) hypothesis, based on his studies of the living fauna, that 'the route of migration lay from the Eastern Himalayas and Assam Hills over the Vindhya-Satpura trend of mountains down the Western Ghats to Ceylon', seems plausible (see also Hora, 1944, 1948). But we have no direct geological evidence in support of such a fascinating hypothesis, and one feels hesitant to reconstruct past geological scenes based solely on the distribution of the existing faunas and floras.

This note has been compiled at the kind suggestion of Dr. S. L. Hora, Director, Zoological Survey of India. I am deeply obliged to him in making available to me a copy of Mr. P. E. P. Deraniyagala's Presidential Address to the Ceylon Association of Science (1946). I am grateful to Mr. Deraniyagala for kindly going through the short note and for his constructive criticism.

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DATING THE PERIOD OF MIGRATION OF THE SO-CALLED MALAYAN ELEMENT IN THE FAUNA OF PENINSULAR INDIA.

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CONTENTS.

BIOLOGICAL EVOLUTION AND TIME.

After studying Zeuner's account of 'Biological Evolution and Time' (1946, pp. 350–385) and his other recent publications on the subject (1943, 1948), it seemed to me possible to date the period of migration of the so-called Malayan element in the fauna of Peninsular India. Though Medlicott and Blanford (1879, p. 375) had attributed this remarkable discontinuous distribution to the refrigeration of climate during the Glacial periods, they were fully aware of the fact that such a large number of genera, species and subspecies of the 'Malayan' stock could not have been evolved in Peninsular India during the Holocene or Postglacial, a period of about 10,000 to 20,000 years. There are, no doubt, some instances in which subspecific differentiation has occurred within about 7,500 years, but on the whole the vast majority of species appear to have remained unaltered during the Holocene. With the climatic fluctuations of the Pleistocene as a driving force for species formation, it has been calculated that the time required for the evolution of two species from their common ancestor was about 500,000 years. After considering the rate of evolution in different groups of terrestrial animals, Zeuner (p. 375) concludes that the fastest rate of species formation lies between 500,000 and one million years and that very few species have existed unaltered for more than one million years.

As a result of his studies, Zeuner (pp. 378–380) has come to certain tentative conclusions, which may be reiterated here for convenience of reference.

1. There appears to be a fastest rate of evolution of species under natural conditions, namely, about 500,000 years per species step.
2. In evolution, the number of generations appears to be less significant than the absolute time.
3. Every species passes through an episode of rapid evolution but may become stabilized thereafter and persist unaltered for a long time.

Changes in the specific composition of a fauna are due both to extinction of older forms and to the appearance of new ones, which may either be immigrants or forms newly evolved on the spot. When environmental conditions change frequently and considerably, species with a fast rate of evolution have an advantage over

slowly evolving forms, with the result that the former may change and survive while the latter may become extinct. With changes in environmental conditions, new characters are bound to be acquired by animals as an adaptive measure and it is likely that these acquired characters become incorporated in the heritage of a species after long periods of time.

Torrential Fishes of Malayan Affinities in Peninsular India.

In the light of the data presented above from Zeuner's work, I shall now discuss the evolution of torrential fishes of Malayan affinities found in the hills of Peninsular India. I have taken up this specialized group of fishes for analysis in view of my own extensive studies on their systematics, ecology and bionomics. We shall first consider the Homalopteridae which exhibit the highest adaptive modifications among Indian hill-stream fishes.

The Homalopteridae are represented in the hills of Assam and Burma and in the Eastern Himalayas by the genera *Homaloptera* van Hass. and *Balitora* Gray. In the hills of Peninsular India, the genera are *Balitora* Gray, *Bhavania* Hora and *Travancoria* Hora. The last two genera are undoubtedly evolved from the generalized form *Homaloptera* and in fact I had myself confused their precise systematic position and even after establishing a new genus for these fishes, referred them to *Homaloptera* subsequently. It was in 1937 that the restricted nature of its gill-openings was noticed and its exact position in the family defined. In no other genus of the Homalopterinae is this character present though restricted gill-openings are characteristic of several genera of the Gastromyzoninae. *Travancoria* has features intermediate between *Homaloptera* and *Balitora*, but there is enough morphological evidence to show that it has evolved from a *Homaloptera*-like ancestor. Both these genera are found in the extreme south of India, thereby showing their antiquity.

The species of *Balitora* found in Peninsular India presents some interesting data. Two species, *B. brucei* Gray and *B. maculata* Gray, are known from the Eastern Himalayas and the Assam Hills, while a subspecies of the former, *B. b. burmanicus* Hora, is known from Burma and the Chittagong Hill Tracts. A second subspecies, *B. b. melanosoma* Hora, closely allied to the first, but differing in colouration, is known from the Siamese-Burmese border. Another subspecies, *B. b. mysorensis* Hora, is known from the Western Ghats above the Palghat Gap and below the Deccan Trap formations. These subspecies occurring to the east and west of the Bay of Bengal are very closely allied and are undoubtedly evolved from a primitive form of *Balitora brucei*. That primitive form must have lived in the hills of Assam and Eastern Himalayas, but as a result of the latest phases of the uplift of the Himalayas it became more specialized for life in torrential streams.

Among the other hill-stream fishes, we find the same degree of differentiation. For instance, generic or subgeneric differences are noted in the case of *Lepidopygopsis* Raj (allied to *Schizothorax* Heckel of Yunnan and the Highlands of Central Asia); *Osteochilichthys* Hora and *Kantaka* Hora (allied to *Osteochilus* Günther of Southern China, Indo-China, Siam, Malay Peninsula, Indo-Australian Archipelago and Burma); and *Nukta* Hora (allied to *Schismatorhynchus* Bleeker of the fresh waters of the Indo-Australian Archipelago). A shorter period of time than required for the differentiation of genera and subgenera was probably required for the divergence of such groups of species as *Thynnichthys* spp. of Sumatra, Borneo, Malay States, Siam, and Indo-China and *Th. sandkhol* (Sykes) of the Godavari and Kistna River Systems; *Mystacoleucus* spp. of China, Siam, Lower Burma, Malay Peninsula, Sumatra, Java and Borneo and *M. ogilbii* (Sykes) of the Deccan; *Batasio* spp. of the Eastern Himalayas, Burma, Siam, Malay Peninsula and *B. travancorica* Hora of Peninsular India; and *Gagata* spp. of Orissa, Bengal, Assam, Burma, Siam and Sumatra and *G. itchkeea* (Sykes) from the Western Ghats.

In the case of one species with remarkable discontinuous differentiation, namely, *Silurus cochinchinensis* C.V., it seems that no differentiation has taken place so far, though the Wynaad and Coorg specimens were at one time assigned to a separate species on the number of barbels. To this category may also be added two other Siluroid species, *Amblyceps mangois* (Ham.) and *Laguvia rebeiroi* Hora, which are found in the Satpuras on the one hand and the hills of Assam, Eastern Himalayas and Farther East on the other. These three species have not undergone any subspecific or specific differentiation.

The above discussion can be summarized in the following table :—

	Indian Peninsular Species.	Allied species in Indo-Chinese and Malayan Sub-regions.
	Family HOMALOPTERIDAE.	
1.	*Balitora brucei mysorensis*	*Balitora brucei brucei.* *Balitora brucei burmanicus.* *Balitora brucei melanosoma.*
2.	*Bhavania annandalei*	*Homaloptera* spp.
3.	*Travancoria jonesi*	
	Family CYPRINIDAE.	
	Lepidopygopsis typus	*Schizothorax* spp.
	Osteochilus (*Osteochilichthys*) *thomassi*	*Osteochilus* spp. Several subgenera but not those found in Peninsular India.
	O. o.	do.
	O. (*Kantaka*) *brevidorsalis*	do.
	Schismatorhynchus (*Nukta*) *nukta*	*Schismatorhynchus* (*Schismatorhynchus*) *heterorhynchus.*
	Thynnichthys sandkhol	*Thynnichthys* spp.
	Mystacoleucus ogilbii This species with a much longer anal fin may form a separate subgenus.	*Mystacoleucus* spp. Differentiated into several subgenera.
	Family SILURIDAE.	
11.	*Silurus cochinchinensis*	*Silurus cochinchinensis.*
	Family BAGRIDAE.	
12.	*Batasio travancorica*	*Batasio* spp.
	Family SISORIDAE.	
13.	*Gagata itchkeea*	*Gagata* spp.
14.	*Laguvia rebeiroi* (Satpuras)	*Laguvia rebeiroi.*
	Family AMBLYCEPITIDAE.	
15.	*Amblyceps mangois* (Satpuras)	

DATING THE PERIOD OF MIGRATION OF THE TORRENTIAL FISHES.

Aquatic animals are not so readily affected by environmental changes as the terrestrial forms and for this reason we may assume that the rate of evolution among the former would be a slower process. Moreover, among the fishes listed above, differentiation seems to have gone further than one species step as new subgenera and genera have evolved since their isolation in Peninsular India. Even taking the slowest rate of evolution for two species steps producing subgenera and genera at about five million years, the date that can be fixed will be well within the Pliocene, the duration of which was of the order of 10 or 12 million years, and which preceded the final geological epoch, the Pleistocene, which lasted for 600,000 to one million years.

There is considerable collateral geological evidence that the specialized hill-stream fish fauna did not invade Peninsular India much before the Pliocene period. Though the freshwater fish fauna of Ceylon is now fairly well known, none of the

genera mentioned above are known from the island though some of them are found in the extreme south of the peninsula. Dr. K. Jacob, Palaeobotanist, Geological Survey of India, has very kindly informed me that

> 'Ceylon remained geographically a part of the Indian mainland until quite recent times. The island was first severed during the Miocene epoch when a wide arm of the Tertiary sea extended across the southern parts of the peninsula. This phase in the geological history of the island is indicated by the marine fossiliferous deposits laid down in the northern and north-western parts of Ceylon extending from Puttalam on the west coast to Mullaitivu on the east including the whole of the Jaffna peninsula in the north. The Puttalam-Jaffna sediments, according to Davis (Wayland and Davis, 1923), may be as late as Pontian or Sahelian (Lower Pliocene) which, geochronologically stated, may probably be as old as fifteen million years. Similar, more or less contemporaneous, depression of land in the neighbouring parts of southern India is suggested by the very closely related Quilon beds of Travancore on the West Coast.'

Though there were land connections between Ceylon and India in subsequent periods and the final severance may be only 10,000 years old, the continuity of hill ranges seems to have been broken in the early Pliocene period, thus the migration of specialized hill-stream forms had stopped since that period. Had the specialized hill-stream fish fauna invaded the peninsula earlier, it would have been able to cross over to Ceylon as is the case with some other older genera, such as *Garra*, *Nemachilus*, *Tor*, etc. By this way also the longest period that can be assigned to the earliest migration of torrential fishes with Malayan affinities can be about 15 million years.

Mode of Dispersal of Torrential Fishes.

Another difficulty in the case of aquatic animals, especially the highly adapted hill-stream fishes, is the mode of their dispersal from the Indo-Chinese Subregion to Peninsular India and Ceylon. Their dispersal can either be by river captures, by the tilting of the land masses consequent on geological processes or some chance dispersal. I think all the three factors have been at work in this region. Gregory (1925) has shown that in the Indo-Chinese Subregion, the rivers on the west, as a general rule, beheaded the rivers on the east and in this process the eastern fauna got dispersed to the west. The Himalayan movements were from north to south but the Assam syntaxis may have influenced the tilting of the area to the west of it. But such river captures and tilting of land masses do not occur very often, in spite of the fact that the orogenic movements that gave rise to the Himalayas had marked influence in the evolution of the present-day geography of India over very long periods and that these movements have not completely died out as yet. The area to be covered is vast and the steps necessary for the dispersal of fishes over this area must have been numerous. The answer can perhaps be found in the ecology and bionomics of hill-stream fishes.

As a rule, the hill-stream fishes of India breed during hot and dry months when the temperature of the water in the hills rises above 75° to 80°F. Most of the breeding thus takes place in April-May when the waters are low and the streams are cut up into shallow pools and puddles with or without streaks of waters connecting them. The young of these specialized fishes are of the generalized type as has already been shown in the case of fishes of the genus *Garra* (Hora, 1921), characterized by the possession of a suctorial disc behind the mouth. The highly adaptive features of the adult develop as the young invade swifter and swifter currents. Another feature of the pools during the dry months is that they are full of young fish in various stages of development and their number in relation to the number of adult fish in the stream is perhaps thousands of times greater. These dry months are followed by heavy monsoons in Indian hills and so long as the relations between the distribution of land and sea were more or less the same as they are today, the present-day conditions can be presumed to have existed in the past also. As a result of monsoon floods, a large number of young fish probably perish and it is

known that some are carried down into rivers. Being of the generalized type and feeding on plankton, they can probably survive for some days in deeper waters. Another factor then comes into play. The hill-stream fishes have the instinct to swim against the current and this instinct is more marked in the young fishes. Thus when young fishes drift down from the hills into rivers in the plain, at the meeting of a tributary lower down they may enter that tributary and work their way up into another hill-stream and there, under proper environmental conditions, may develop into their characteristic adult form, and thus year after year there may be chances for the extension of the range of the species. What is necessary is the continuity of hilly conditions so that torrential streams occur all along its route of dispersal. When these conditions are interrupted in any part of the route, isolation results and new forms are then evolved. From the affinities of the fish fauna listed above, it seems that continuous dispersal between the Assam Hills and the Satpuras continued for long geological periods comprising late Tertiaries and Pleistocene and that discontinuity between these hill ranges is of a recent occurrence.

SPECIATION AMONG TERRESTRIAL ANIMALS.

Mammals.—The genus *Moschothera* Pocock has two species which are closely allied and even regarded as races of the same species. *M. megaspila* (Blyth) is found in central and southern Burma, Malay Peninsula, Siam and southern Indo-China. *M. civettina* (Blyth) occurs in the Western Ghats. The divergence in these two forms may have occurred during the Pleistocene. The same is true of the two species of *Charronia* Gray. The Himalayan *C. flavigula* (Bodd.) and the South Indian *C. gwatkinsii* (Horsf.) are just sufficiently distinct to be separated into two species. The two Indian species of *Hemitragus* Hodgson, one found in the Himalayas (*H. jemalicus*) and the other in the Western Ghats (*H. hylocrius*), have the same type of distribution and their differentiation is also of the same order.

Birds.—Among the birds we get gradation of differentiation. For example, *Irena puella* Latham (Fairy Bluebird), *Arachonothera longirostris longirostris* (Latham) (Spider Hunter), *Alcemerops athertoni* (Jar. & Selby) (the Blue Bearded Bee-eater) and *Dichoceros bicornis* (Linn.) (the Great Indian Horn-bill) are found on both sides of the Bay of Bengal without undergoing even subspecific differentiation. There are other species in which subspecific differences have been observed. These are:—

	Indo-Chinese and Malayan Subregions.	Peninsular India.
1.	*Dryocopus javensis javensis* (Horst.) " " *feddeni* (Blyth)	*D. j. hodgsoni* (Jerdon).
2.	*Vivia innominatus* (Burton) (two races)	*V. i. avunculorum* (Hartert).
3.	*Lyncornis cerviniceps cerviniceps* Gould	*L. c. bourdilloni* Hume.
4.	*Tephrodornis gularis pelvica* (Hodgson)	*T. g. sylvicola* Jerdon.

There is still a third category of birds in which specific differentiation has occurred in the two regions as a result of isolation. These genera are *Garrulax* (Laughing Thrushes), *Trochalopteron, Oreocincla, Hemicircus* and *Batrachostomus*.

All the birds referred to above are of evergreen biotope and of tropical and subtropical rain forests. The entire assemblage of birds with Malayan affinities in Peninsular India, from the nature of differentiation detailed above, is probably not more than a million years old. Further in the degree of differentiation, we have evidence of several waves of migration at different periods. In this connection, attention may be invited to Ripley's article on 'Avian relicts and double invasions in Peninsular India and Ceylon' to be published shortly in *Evolution*.

Turtles and Tortoises.—*Geoemyda tricarinata* is common to the Assam Hills and the Chota Nagpur Plateau; *G. trijuga* and *Lissemys punctata* are represented by different subspecies in the two areas; while in the case of *Testudo travancoria* and *T.*

elongata we have two very closely allied species. In any case, differentiation in these forms has not gone beyond a species step and, therefore, their isolation may not be older than a million years.

Snakes.—As in the case of birds, certain species, such as *Dryocalamus gracilis* and *Dryophis nasutus*, are still common to both regions. In certain other species, the differences in the forms found in the two regions are very slight. In *Ahaetulla ahaetulla ahaetulla* and *Chrysopelea ornata* differences in colouration only distinguish the Peninsular Indian forms from the Indo-Chinese or Malayan forms. In *Boiga ceylonensis*, a polytypic species, the differentiation is of a subspecific rank. There are, however, several closely allied species occurring in the two regions, such as *Cylindrophis maculatus* and *C. rufus*; *Chrysopelea taprobanica* and *C. paradisi*; *Dryocalamus nympha* and *D. davisoni*; *Atretium schistosum* and *A. yunnanensis*; and *Rhabdops olivaceus* and *R. bicolor*. In no case has differentiation been noticed beyond the species step and it seems that the two faunas have not been isolated for any very long period.

Lizards.—Among lizards there is a much larger number of species which have remained unaltered so far in the two regions. Such species are *Cnemaspis kandiana*, *Hemidactylus frenatus*, *H. bowringi*, *Platyurus platyurus*, *Gehyra mutilata*, *Hemiphyllodactylus typus typus*, *Lepidodactylus lugubris*, *Mabuya macularia* and *Riopa lineata*. Then we have groups of allied species occurring in the two regions, such as *Draco dussumieri* and *D. norvilli*; *Cophotis ceylanica* and *Cophotis sumatrana* of Java and Sumatra; *Draco subcaerulea* and *D. olivacea*; *Lygosoma dussumieri* and *L. maculatum*; and *Riopa albopunctata* and *R. bowringi*. Here again, there is nothing beyond one species step, so the isolation of the two faunas may have taken place during the Pleistocene.

Annelida.—Among the Annelida also we find species and subspecies common to the two widely separated areas, exception being *Drawida travancorensis* and *D. jalpaigurensis*. Species like *Drawida pellucida pellucida*, *Herpobdelloidea lateroculata*, *Myxobdella annandalei*, *Haemadipsa zeylanica zeylanica* and *H. montana* are found in both regions though totally absent from the intervening areas.

CONCLUSIONS.

It will be seen from the above that except in the case of the most specialized torrential fishes, the Homalopteridae and the Schizothoracinae, the differentiation between the two faunas has proceeded only as far as the first species step. In all other groups of animals discussed above, the migration of these forms and their isolation from the parent stock would seem to be a matter of, at the most, a few million years, so the topographical and climatic features contemplated in the Satpura Hypothesis (Hora, 1937, p. 255; 1944, p. 429) may have persisted during the Pliocene and Pleistocene periods.

If the dates fixed above on the data of animal speciation are even approximately correct, it follows that no other theory except the Satpura Hypothesis can account for the dispersal of Indo-Chinese and Malayan forms to Peninsular India. This theory contemplates that the Satpura and Vindhya trend of mountains was once more pronounced, damp and continuous with the Assam Hills and the Eastern Himalayas in the east and with the Western Ghats in the west, and served as a route of migration of the specialized hill fauna and flora from the east to the west. There was never a land connection across the Bay of Bengal even during the Tertiaries (70 million years). The Satpura Hypothesis, as proposed and developed by the writer, is, therefore, the only possible explanation of this remarkable discontinuity in the distribution of the fauna of India.

It may be noted that dampness, rather than any other climatic factor, has been responsible for the dispersal of terrestrial 'Malayan' forms to Peninsular India. The last and third phase of the last Glaciation occurred about 23,000 years ago.

It was probably connected with the second phase, which started 70,000 years ago, by an interstadial, which in the north was pronouncedly cool. It is quite possible, therefore, that for a period of about 50,000 years prior to 20,000 years ago the climate was more humid in the peninsula and favoured the dispersal of the terrestrial forms referred to above. It is not improbable, therefore, that whereas the aquatic forms began to migrate to South India a few million years ago, the terrestrial forms mostly migrated during the above-noted 50,000 years of damp climates in India.

ACKNOWLEDGEMENT.

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PRECIPITATION ON MOUNTAIN SLOPES.

By S. K. BANERJI, *O.B.E., D.Sc., Director-General of Observatories, India Meteorological Department, New Delhi.*

Pockels (1901) has computed the rainfall distribution on mountain slopes. The mountain profile is represented by

$$\eta = C \sin mx\, e^{-r\eta},$$

where—

x is the horizontal distance measured normal to the mountain-range,
η gives the height of the mountain profile,

$m = \frac{\pi}{\lambda}$, λ being the horizontal distance between the centre of the valley and the summit of the mountain,

$r = \sqrt{m^2+q^2/4}$,

q being a constant equal to 1/8000. C determines the height of the range. The values of C and m are so chosen that the equation roughly represents the profile of the particular mountain.

Correspondingly, the vertical velocity (v) of the wind is given by the expression,

$$v = Cam \cos mx\, e^{-nY},$$

where Y is the vertical co-ordinate.

The constant a is related to the horizontal velocity of wind (u) by the expression

$$u = a(1 + C\frac{m^2}{m} \sin mx\, e^{-nY}).$$

We also have

$$n = -\frac{q}{2} + r.$$

The rate of precipitation (W) is given by

$$W = -\int_{Y^0}^{Y'} v\epsilon F'(Y)\, dY,$$

ϵ being the air density.

$F\ (Y)$ is the specific humidity of saturated air at the altitude Y.

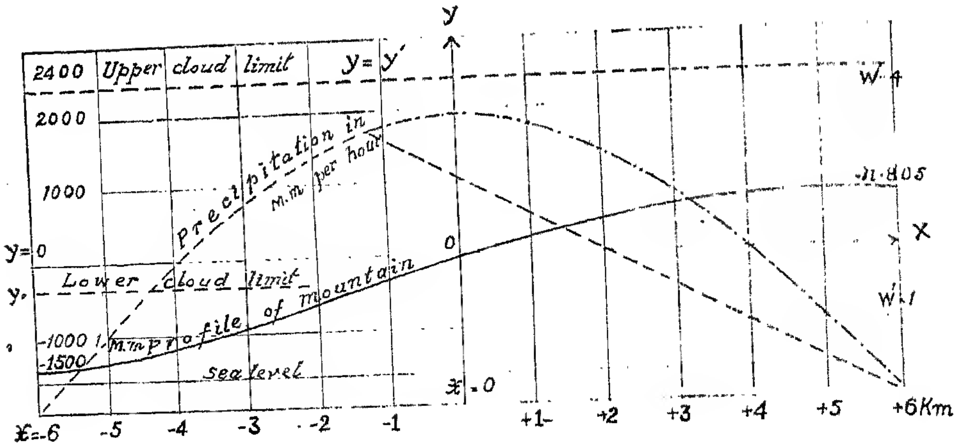
Y^0 and Y' are respectively the heights of the cloud base and cloud top.

In computing the rate of precipitation Pockels assumes that the products of condensation simply fall vertically without being carried along by the horizontal current of air. The diagram on the next page shows the variation in the precipitation rate along a mountain slope for a case computed by Pockels.

In applying Pockels's theory to the Satpura range, the following values have been used :—

Horizontal distance from the valley to the summit (λ) = 80 kms.

The present height of the top of the range, above the centre of the valley is taken as 800 metres or 2,600 feet. The corresponding value of C is 400 metres. (The hill



tops of the Satpuras are about 3,600 feet above sea-level and the surrounding valley is about 1,000 feet above sea-level. Hence the hill tops are 2,600 feet above the valley level). The monsoon air is taken as having an average temperature of 80°F. and relative humidity of 80%. The amount of precipitation depends on the thickness of the cloud layer. The monsoon clouds may be taken to have the base at 400 metres and the top at 4,000 metres or 5,000 metres depending on the region under examination and state of the monsoon. Assuming that the cloud base is at 400 metres and cloud top at 4,000 metres above the valley, the maximum rate of ... conditions is found to be $10a/g$, where g is the

... value of the monsoon rain on the Satpuras is 70″ which occurs at ..., the height above sea-level being 3,528 feet. If we assume that 70″ determines the maximum rate of rainfall on this mountain slope during the monsoon period which we call W_1, we get

$$10a/g \propto 70 \quad \text{or} \quad 10ak/g = 70 \quad \text{or} \quad \frac{ak}{g} = 7$$

where k is a constant.

It may reasonably be assumed that the value of a depends only on the general airflow and will not be affected by any limited changes in the height of the range. a can therefore be regarded as a constant.

The equation $\frac{ak}{g} = 7$ can thus be used for computing the likely monsoon rainfall when the height of the range is altered.

By similar computation, it is found that when $C = 800$ metres, i.e. when the height of the range is 5,300 feet above the valley or 6,300 feet above sea-level, the maximum rate of precipitation is 30 a/g. The cloud top is now taken as at about 5,000 metres. The corresponding monsoon rainfall will be 22 $\frac{ak}{g}$. Substituting $\frac{ak}{g} = 7$, we get the total monsoon rainfall as 154″. Thus, if the Satpuras are about 6,000 feet high above sea-level, the monsoon rainfall is likely to be about 150″ at a height of 4,000 feet above sea-level on the hill slopes.

When $C = 1,100$ metres, i.e. when the height of the range is 7,300 feet above the valley or 8,300 feet above sea-level, the maximum rate of precipitation is 27 a/g.

The cloud top is again taken as at 7,000 metres above the valley. The corresponding monsoon rainfall will be $27 \frac{ak}{g} = 27 \times 7 = 189$.

If the Satpuras are of a height of about 8,000 feet above sea-level, the monsoon rainfall is likely to be about 200″ at a height of 5,000 feet above sea-level on the hill slopes. We thus get the following results :—

Height.	*Rainfall.*
For the present height of 3,600′ a.s.l.	70″
If the height is 6,000′ a.s.l. ..	150″
If the height is 8,000′ a.s.l. ..	200″

Therefore, if the height of the Satpura range be extended to 8,000 feet, one could expect on theoretical consideration a maximum possible precipitation of 200″ per annum. Taking this to represent roughly the average rainfall over Western Ghats, it would appear that the Satpura range will have to be raised to about 8,000′ to get this precipitation.

The above values should be regarded as indicating orders of magnitude only. These are the maximum possible values given by theory. In practice, the whole of it may not be realized, although a large part of it will be realized. The rainfall in other than monsoon months is small in this area and the values of monsoon rainfall given here may be taken to be very nearly equal to the annual rainfall.

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CLIMATE OF INDIA IN RELATION TO THE RAINFALL DISTRIBUTION.

Note prepared under the direction of the Director-General of Observatories.

The accompanying map shows the distribution of annual rainfall over India. The climatic zones into which the various rainfall areas may be divided are shaded.

Annual Rainfall of more than 75 inches.

There are two areas which have more than 75″ annual rain—one along the West Coast of the Peninsula and the other in north-east India. There are, however, appreciable differences in the climatic features of the two zones. The rainfall along the West Coast is almost entirely confined to the Monsoon Period. In north-east India most of the rainfall is during the Monsoon period but an effective amount also falls during the Summer months, March to May. Temperatures in north-east India are lower by 15°F. in winter and higher by 5°F. in Moonson, than along the West Coast. Relative humidity is high in both the areas. Daily range of temperature is small along the West Coast throughout the year. In north-east India, the daily range is greater in Winter and the premonsoon months.

In both the areas there are zones which get 200″ of rain or more, but the climatic conditions as judged by air temperature and humidity are not considerably different from zones getting 100″ rain.

In the rain-shadow of the Khasi hills there is a small area which has a rainfall between 50″ and 75″ but its climate is nearly the same as that of the adjoining areas which have a greater rainfall.

Annual Railfall between 50 inches and 70 inches.

The rainfall is between 50″ and 70″ along south-east Madras coast, in West Bengal, Orissa and West Central Provinces and in a narrow belt along the Himalayas to the west of 87°E. They form three climatic zones—south-east Madras coast, Himalyas to the west of 80°F. and the rest.

South-east Madras coast gets much of its rain from October to December and is warm throughout the year. Daily range of temperature is small. Relative humidity is generally high, though in the South-West Monsoon period it is less humid than the area to the North.

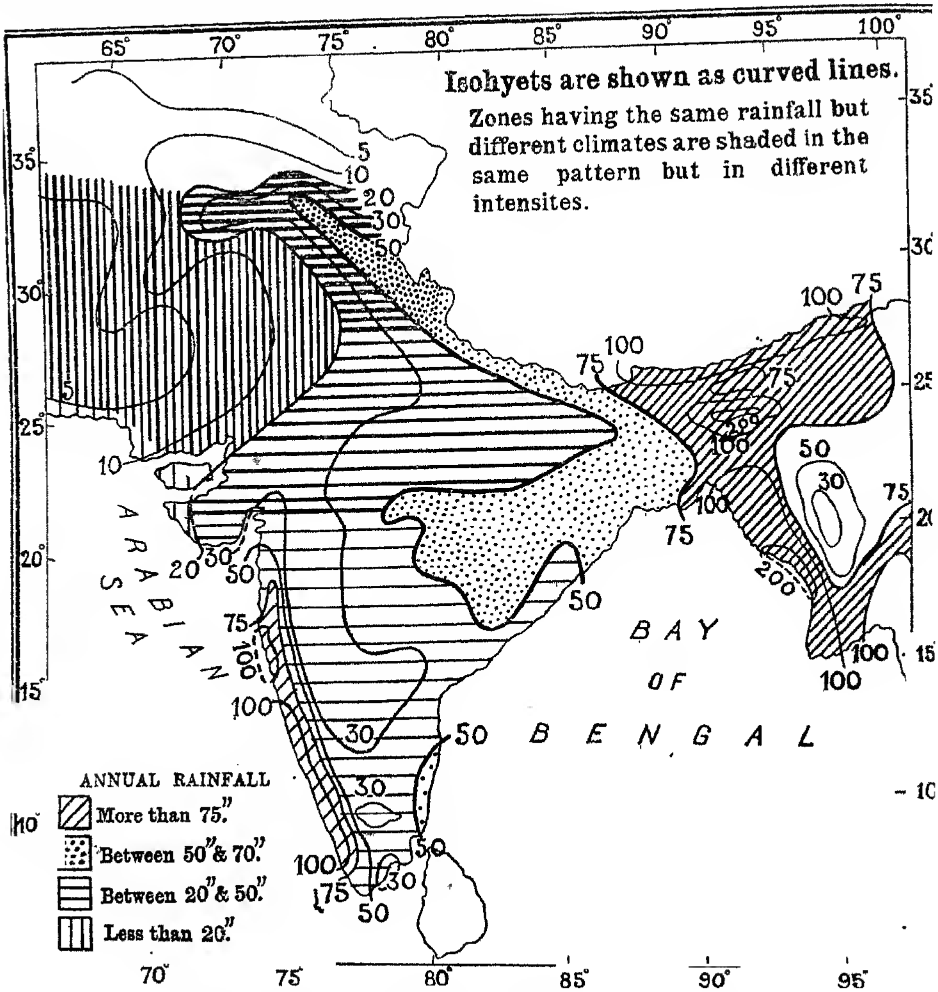
The Himalayan zone to the west of 80°E. receives the major portion of the annual rainfall in the Monsoon but an effective amount also falls from December to May. Winter is very cold but the plains become hot in Summer and Monsoon. The daily range of temperature is moderately large. Relative himidity is high during Monsoon and Winter but less in other periods.

The rest of the area gets its rainfall almost wholly in the Monsoon period. It is cold in Winter but becomes hot before the onset of the Monsoon. Diurnal variation of temperature is large except during Monsoon. Relative humidity is high in the Monsoon period but is less in other periods.

Annual Railfall between 50 inches and 20 inches.

The area having this rainfall stretches from Cape Comorin through the central parts of the country to N.W.F.P. It may be divided into three climatic zones—south of 22°N., between 22° and 29°N. and north of 29°N.

The zone south of 22°N. is in rainshadow during South-West and North-East Monsoons. Most of the rainfall occurs between June and October. The zone is warm in winter and hot at other times. Daily range of temperature is moderate to large but less during Monsoon. Relative humidity is moderate to high in the South-West Monsoon period but low at other times.



Climate of India in relation to Rainfall Distribution.

The zone between 22°N. and 29°N. receives all the rain during the Monsoon period June to October. It is cold in winter and very hot in summer. The daily range of temperature is large except in the Monsoon period. Relative humidity is low but increases during the Monsoon.

North of 29°N., there is an effective amount of rain from December to May, though a large part of the annual rainfall occurs during the Monsoon period. It is very cold in winter and very hot during summer. Daily range of temperature is large. Relative humidity is moderate but increases during the Monsoon period.

Annual Railfall less than 20 inches.

Most of North-West India has a rainfall of less than 20″. It may be divided into two climatic zones—the coastal strip and the rest of the area.

Compared to the interior, the temperature and its daily range are moderate and relative humidity higher along the coastal strip. The interior is characterized by extremes of temperature and a large daily range of temperature. Relative humidity is low. The Baluchistan plateau in spite of the elevation records high temperature in summer.

Significance of terms used.

The significance of the terms used in describing temperature, daily range of temperature and relative humidity is as follows:—

Temperature.		*Diurnal Range of Temperature.*		*Relative Humidity.*	
Very cold ..	less than 60°F.	Low or small	less than 20°F.	Low or small	less than 50%
Cold	60–70°F.	Moderate ..	20–25°F.	Moderate ..	50–65%
Warm	70–80°F.	Large or high	more than 25°F.	High ..	more than 65%
Hot	80–90°F.				
Very hot	more than 90°F.				

Temperatures mentioned refer to sea-level. With elevation temperature decreases in the free air at a mean rate of about 3°F. per 1,000 feet. In considering temperatures over hills, the decrease has to be taken into account.

In thickly vegetated areas temperature and humidity conditions may be appreciably different from neighbouring open areas, particularly if the air is likely to be stagnant. The daily range of temperature is smaller and relative humidity is higher in such vegetated areas.

CLIMATES AS AFFECTING THE SATPURA HYPOTHESIS.

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(*Note prepared from the information supplied by the India Meteorological Depratment, New Delhi.*)

In the preceding article on 'Climate of India in relation to the Rainfall Distribution', a general account is given of the relationship of rainfall incidence and climate throughout India but in this article special attention is drawn to the likely routes of migration of the 'Malayan' element in the fauna of Peninsular India and Ceylon and the climatic changes that may have occurred during the glaciation phases of the Pleistocene period.

The Satpura-Vindhya Track.

After analysing monthly normals of rainfall for 17 stations and data regarding the mean temperature and humidities of a few of them along a track extending from the Eastern Himalayas and Assam through the Chota Nagpur plateau and the Narbada and Tapti valleys to the Malabar coastal strip, it has been ascertained that there is considerable similarity between (*a*) the Assam hills and the Eastern Himalayas, (*b*) Chota Nagpur plateau (Ranchi and Hazaribagh districts), and (*c*) the Malabar Tract of the Western Ghats, but considering the relative durations of the rainy seasons and other climatic factors, such as temperature and humidity, the three regions show marked differences. For instance, there is greater similarity of rainfall between Assam and the Western Ghats in southern India than between either of them and the Chota Nagpur hills. In the intervening hill tracts, as one passes from the Chota Nagpur along the Vindhyan and Satpura ranges and tehn down along the Western Ghats to the Nilgiris, the changes in climate are even more marked. A brief climatic survey of the whole belt is given below.

Assam.—The most characteristic feature of the climate is its dampness at all seasons in conjunction with the moderately high and comparatively equable temperature due to its subtropical position and its being protected from desiccating winds by the hills around. The rainy seasons extend from April to November and generally there is copious rain, the higher elevations getting over 100 inches of rain, while the plains may get anything between 70 inches and 100 inches. The mean temperature in the plains is about 75°F. and the thermometer very rarely rises above 100°F., if at all. Mean annual humidity is 80%.

Chota Nagpur.—As we pass westwards to Chota Nagpur hills, we come to a region of annual rainfall of about 50–60 inches. The rainy season is definitely shorter and confined to June to September with a few showers in May and October. The sea-level mean temperature is about 80°F. with a mean annual humidity at 65%. During the rainy season, this region has the same climate as Assam, while in other seasons it is definitely drier, and hotter (except for two months in winter).

Central Indian Plateau, Narbada and Tapti Valleys.—Proceeding westwards we pass on to the Narbada and Tapti valleys. This plateau can be divided into two parts, the eastern and western. The rainfall decreases as one proceeds westwards. Near the headwaters of the Narbada and Sone, the annual rainfall is 50–60 inches. Along the Narbada valley the rainfall near the eastern end is 50″ but diminishes to between 30 and 40 inches near Khandwa. The Tapti, which is south of the Satpura, has in general smaller rainfall in its basin. In Berar and Khandesh the rainfall is 30″ or lower. Where the Tapti basin skirts the northern boundary of the Western Ghats or Sahyadri, the rainfall increases to 40–50 inches.

Mean annual temperature is about 79 or 80°F. in the eastern part of the belt and slightly higher in the western half from Mahadeo hills onwards. Also the

diurnal range of temperature is higher in the west than in the east. Relative humidity also decreases westwards in the belt.

The West Coast of India, Konkan and Malabar.—The strip of hilly and undulating country that extends below the Ghats from the Gulf of Cambay to Cape Comorin has the dampest and most uniform climate of any part of the Peninsula. The rainfall of the summer season (which on the main is from June to September) is heavy all along the coast and still heavier on the Ghats which force the saturated current to ascend to a height of from 2,000 to 7,000 feet before pursuing its course across the tableland. There are also loftier hills such as the Nilgiris, Anamalais and Palnis. This causes enormous precipitation on the face of the Ghats, which at places exceeds 200 inches. On the coast the rainfall is less. From June to October it comes to 119 inches at Mangalore and 132 inches at Honavar where it is heaviest decreasing thence northwards to 100 inches at Ratnagiri and 73 inches at Bombay and to only 42 inches at Surat. Rains set in somewhat earlier and stop later in the south than in the north.

The annual mean temperature along the west coast is the same, namely 70 or 80°F., but there are differences in other respects between the northern and southern parts of the strip. The annual range of temperature is greater in the north than in the south.

It would thus appear that in passing from Assam to the Western Ghats along the route Chota Nagpur to the Narbada and Tapti valleys and the Sahyadri, one has to pass through rather dissimilar climatic regions. One point regarding temperatures and humidities requires special mention. Temperatures, both dry bulb and wet bulb, are recorded for meteorological purposes in Stevenson Screens and represent free air temperatures on more or less open ground. On such ground, both the daily as well as seasonal variations of temperature and humidity, are markedly larger than in forested areas. When considering the problem of migration of animals under natural conditions, one should consider perhaps the micro-climates of forest regions, such as one imagines would have existed in pre-historic days throughout a large part of India. Even if a certain part of the country might be dry in some months and might on that account be not favourable for migration, favourable seasons might be taken advantage of for the movement.

Chota Nagpur, Orissa, Jeypore, Eastern Ghats and Mysore Plateau Track.

There is another belt of country from Chota Nagpur hills through the Orissa and Jeypore hills and the Eastern Ghats to the Mysore plateau and the Nilgiris which affords an equally favourable track for migration of animals and it is likely that, after crossing over from the Assam hills to the Chota Nagpur hills, migration was availed of by terrestrial animals.

The track from Chota Nagpur hills to the Nilgiris *via* Eastern Ghats lies in the following regions:—

(*a*) Chota Nagpur hills; (*b*) Mahanadi valley; (*c*) Jeypore hills; (*d*) Godavari and Krishna valleys; (*e*) Mysore Plateau; (*f*) the Nilgiris and Coorg.

A brief climatic survey of the above regions is given below.

(*a*) *Chota Nagpur Hills.*—This is a region of annual rainfall of about 50–60 inches. The rainy season is confined to June–September with a few showers in May and October. The mean temperature on the hills is about 75°F. with a mean annual humidity at 65%.

(*b*) *Mahanadi Valley.*—This region gets more rain than Chota Nagpur hills, the annual rainfall being 60–70 inches. Out of which about 80% falls during the months June to October. The mean temperature of the year is 80°F. and the mean relative humidity is 60% generally.

(c) *Jeypore Hills*.—As we pass southwards to Jeypore hills, rainfall decreases, the mean annual rainfall being 61 inches at Jagdalpur. But it is interesting to see that the May to November rainfall is about 50 inches both in the Mahanadi valley and Jeypore hills. The mean temperature is about 75°F. the same as in the Chota Nagpur hills and the mean relative humidity is about 65%.

(d) *Godavari and Krishna Valleys*.—Coming to this region we pass on to an area of definitely less rain. The mean annual rainfall is 30 to 40 inches decreasing from north to south. Most of the rain falls during the months May to November. Mean temperature of the day is slightly higher being 81–82°F. but the mean daily relative humidity is, however, the same as for Jeypore hills.

(e) *Mysore Plateau*.—Rainfall conditions here are more or less the same as in the Godavari Krishna valleys, the annual rainfall being 30 to 40 inches increasing towards south. About two inches more of rain falls during the months December to April in this region than in the previous region. Being a plateau the mean temperature of the layers of the atmosphere near the surface of the earth is 75 to 78°F., slightly cooler than the neighbouring plains. The mean relative humidity is the same as in the previous region being 60–70%.

(f) *The Nilgiris and Coorg*.—Rainfall rapidly increases towards west and at Mercara the annual rainfall is 125 inches. The mean annual temperature at Mercara is 68°F. and the humidity is greater than 70%.

It will be seen from the above that along this track the rainfall is less in the middle than at the two ends, and the conditions of temperature, humidity and duration of rainy season are more uniform as at present than along the Satpura track. Though evidence of fish migration along this route is lacking, there is some evidence among birds and other terrestrial organisms.

Glaciation and Climatic Changes.

During the one million years of the Pleistocene period, the earth witnessed three periods of glaciation and its regression, and these had no doubt great influence on the climate of India, thereby resulting in the dispersal of animals. It may be remembered at the outset that there is no climatological factor that has greater influence on the dispersal of animals than humidity and in the following account particular attention will, therefore, be paid to this factor.

The extent of glaciation in India can be judged from the fact that glaciers never descended to below 5,000 feet in the Himalayas. The seas round India had a drop of temperature from 28°C. to 20°C.

Though it is very difficult to say with any confidence what the climate might have been during the 'Pluvial periods', one can only make a plausible conjecture. At present Himalayan glaciers commence at about 12,000 feet. During the glacial periods their level came down to 5,000 feet, *i.e.*, by 7,000 feet. At an average lapse rate of 6°C./km., which is equivalent to a decrease of 12°C. or 21°F. in the temperatures over India during the glacial period compared to the present. The mean temperature in May, the hottest month, at Nagpur is now 97°F. In the summer of the glacial period the temperature might have been about 76°F. which is comparable with the present December temperature of 68°F. at Nagpur. Thus the temperature conditions during the summers of the glacial periods would have resembled the present winter conditions.

At present, over Asia the winter anticyclone is replaced in summer by a low pressure area with the lowest pressure somewhere over north-west India. This is essential for the development of the South-West Monsoon. In the glacial periods, it is probable that glacial anticyclones might have prevailed throughout the year and might have prevented the development of South-West Monsoon as we know it now; or the Monsoon circulation, if at all existent, might have been very weak and its seasonal rainfall comparatively little.

With a glacial anticyclone over Asia all through the year, conditions would have been favourable for a 'front', similar to the winter Mediterranean Front. Such a front might have remained for the greater part of the year across the central parts of India. In such a situation depressions, of the type of our present-day winter, might have formed and moved from west to east along this front.

As regards the effect of cooler oceans let us try to picture the consequences. A decrease in the sea temperatures from 28°C. to 20°C. is calculated to produce a 40% decrease in the moisture that can be picked by air currents from the sea. Thus, even if the South-West Monsoon prevailed in the glacial period the associated rainfall would probably have been appreciably less than at present.

In the glacial period there might not have been any South-West Monsoon or if at all existent, it might have been very weak. Hence the heavy rain that now falls along West Coast and parts of Ceylon in a period of about four months during the South-West Monsoon might have been absent in the glacial period. Also, the North-East Trade Winds might have blown all through the year and been more vigorous than at present. These Trades might have given more rain in the East Coast plains and the eastern slopes of the hills than to the West which would be in the rainshadow of the Trades. This rainfall might have been more or less evenly distributed throughout the year. This means that in the Peninsula south of 15°N., there might have been more rainfall in the eastern portions and less rainfall in the western portions as compared to the present conditions.

Regarding temperatures in the glacial period in the tropics and equatorial regions, it seems to be the opinion of Brooks that the temperatures in the glacial period were not appreciably lower than at present; at least not by as much as in the northern latitudes. Purely from a meteorological point of view, it is difficult to say anything about the temperatures in the tropics.

With the great development of snow and ice on the Himalayas during the glacial period, the glacial anti-cyclone over the continent of Asia would have extended up to about 30°N. latitude over a large part of the year. This would have caused an easterly flow, bringing to some extent moist air from the Bay of Bengal. Also, the extension of the cold areas over a large part of the present temperate regions would have brought the 'Polar Front' between the polar east winds and temperate west winds nearer to the equator, and by increasing the temperature contrast between low and high latitudes would have increased the storminess. Moist air would have drawn into these storms. Both the easterly flow and the increased storminess would have maintained the relative humidities during the glacial period about the same as at present.

Conclusions.

It would appear highly probable from the above that though the temperatures might have been less during the glacial periods, the relative humidities in Peninsular and north-east India were of a fairly high order or at least continued to be of the same order as at present. Further, these humid conditions were more uniformly distributed all over India, particularly in the south, and thus favourable conditions existed for the dispersal of moisture-loving, terrestrial animals during the 'Pluvial' periods. The succession of Pluvial and Arid periods seems to have influenced successive waves of migration of terrestrial animals and thus there is evidence among the birds at least (Ripley, 1949) of a double or triple invasion of the Peninsula by the fauna from the east. Though with high humidities even in the plains of India, for the dispersal of terrestrial animals the Garo-Rajmahal Gap need not be bridged over to form a continuous series of mountain ranges as postulated in the Satpura Hypothesis, the distribution of torrential fishes and other hill-stream organisms cannot be accounted for on the basis of high humidities and thus alteration of certain topographical features is necessary to account for their dispersal during the Pliocene and Pleistocene periods. The Satpura Hypothesis therefore not only meets this contingency but will also account for high humidities along the postulated route of migration.

BOTANICAL NOTES ON THE SATPURA THEORY.

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(Communicated by Dr. S. L. Hora, F.N.I.)

The flora of the Chota Nagpur plateau differs considerably from that of the Gangetic plain to the north and Orissa to the south. The floristic composition shows that the area is, as it were, a meeting place for the plants of Bengal proper, Orissa and Eastern Himalayas. The soil of micaceous schist and quartz favours the formation of dry deciduous jungle of mixed forest with associes of Sal, Terminalia, Anogeissus, Acacia, Anacardium occidentale, etc. But it is in some of the higher hills, on account of their elevation and increased humidity, species of a damp tropical flora exist in isolated patches. In this connection particular mention must be made of the relic vegetation on the Parasnath hill top, the flora of which according to our recent studies finds a more or less close parallel with that of Kurseong in the Darjeeling district. Of this tropical flora Hooker (1875; 1904) says 'Of plants eminently typical of a moister atmosphere I may mention the genera Bulbophyllum, Begonia, Aegenetia, Disporum, Panax, Eugenia, Myrsineae, Ferns and Mosses and foliaceous lichens which appeared in strange association with such dry climate genera as Kalanchoe, Pterospermum, and the dwarf palm *Phoenix acaulis*. Added to this list the species of *Berberis asiatica, Clematis nutans*, Thalictrum, grasses and Cardamine on the mountain top represents a mixture of plants of damp hot, dry hot and temperate climate in fairly balanced proportion'. Clarke (1898) considers that geographically the Parasnath Hills are a prolongation of the north-eastern edge of the Deccan plateau into the Gangetic plain. Considering the occurrence of so many sub-Himalayan plants in association with those of the drier plain regions, the view has long been entertained that Parasnath and other hills of Meghasani group in the southern tract which rise abruptly to great heights from the plains of Bihar might have served as stepping stones for the mutual exchange of plants between the Deccan and the Eastern Himalayas. Similarly, Haines (1921–25) has suggested that the parts of Ranchi and Hazaribagh 'may have served as stepping stones for the passage of species from the highlands of the Peninsula to the newer Himalayas or in some cases in the reverse direction'. Mooney (1944) has recently reported from the pats of Jashpur and Surguja the occurrence of *Crataegus crenulata, Pyrus pashia, Berberis asiatica, Cudrania javanica,* at an altitude of 3,700 ft. The normal habitat of these are the temperate Himalayas from Kashmir to Bhutan and the Khasi hills and Manipur. The occurrence of *Rubus ellipticus* has also been reported from the Mayurbhanj hills and from the Kasipur plateau in Kalahandi State.

The inner highlands of Orissa like that of Chota Nagpur form a plateau with some of the higher hills reaching subtemperate altitudes. The ghats that lead up to these highlands are continuous to the north with the eastern escarpments of Chota Nagpur and to the south with the mountains of the Eastern Ghats. The submontane strip below is continuous to the north with the drier part of West Bengal. The flora of Southern Orissa in general is of the Peninsular type with a number of species common to the Coromandel Coast. However, Mooney (1947) has recently recorded 13 species of Rosaceae from the hills of Bihar, Orissa and neighbouring States which are of some interest. These are *Pygeum acuminatum, P. Andersonii, P. Mooneyi, Rubus ellipticus, R. lasiocarpus, R. rugosus, Fragaria indica, Potentilla Kleiniana, P. Leschnaultiana, P. supina, Rosa involucrata, Pyrus pashia, Crataegus crenulata.* Rosaceae are generally denizens of the northern temperate

climates and in India, they are generally found in the Himalayas. But some are also found on the higher elevations of the Nilghiri and Pulney Hills and Western Ghats. Mooney regards the new habitats of some members of Rosaceae which are intermediate between the great Himalayan mountains on the north and the Nilghiri Hills in the south as indicating a southerly migration of the Himalayan species to the highlands of the Nilghiris and Travancore.

The sholas of Nilghiri Hills are rich in species which have affinities with that of the cool regions of the far distant Khasia, Manipur and Naga Hills and Southern Burma. Amongst trees and shrubs common to these localities and most of them to the temperate Eastern Himalaya also are *Ternstroemia japonica, Hypericum Hookerianum, Hypericum nepalense, Eurya japonica, Rhamnus dahuricus, Photinia notoniana, Rubus ellipticus, R. lasiocarpus, Carallia brachiata, Rhododendron arboreum, Gaultheria fragrantissima,* and *Gardneria ovata* together with species of Kadsura, Berberis, Pittosporum, Elaeocarpus, Euonymus, Meliosma, Pygeum, Rosa, Viburnum, Lonicera and Vaccinium. The herbaceous plants common to the Khasia and the Nilghiris are mostly European genera and species, like Thalictrum, Ranunculus, Cardamine, Geranium, Alchemilla, Fragaria, Scutellaria, Potentilla, Parnassia, Lysimachia, Swertia, Gentiana, many Cyperaceae and grasses.

The flora of the Eastern and Western Ghats of the Deccan plateau is interesting from the point of view of indicating affinity with the Malayan region. The south-western province of Malabar is characterized by the presence of Guttiferae, Dipterocarpaceae, Myristicaceae, Helicia and many palms and Bamboos. The great excess of Malayan types, in families like Sterculiaceae, Tiliaceae, Anacardiaceae, Meliaceae, Myrtaceae, Melastomaceae, Ampelidaceae, Gesneraceae, Piperaceae, Scitaminaceae, Orchidaceae and Araceae is very evident. *Podocarpus latifolia* occurring in Burma and Malay peninsula has been reported from Tinnevelly hills. From the published flora of Travancore it is known, that it has close affinities with the flora of Ceylon which is predominantly Malayan. The distribution of genera such as *Dipterocarpus, Grewia, Dioscorea, Gaultheria,* which are found in large numbers in tho forests of Burma are confined mainly to this region of India.

A retrospect of the main vegetational features of the mountain ranges of peninsular India shows that the flora is closely akin to that of Sikkim, Bhutan, Assam and Burma. The higher hills of Chota Nagpur and Orissa indicate the gradual succession of vegetation from the dry hot climate of the plains to the temperate elevation of the hill tops where characteristic relic vegetation of Himalayan and Malayan species occur. The presence of so many Himalayan and Malayan species in the hills of Chota Nagpur and Orissa is explained as indicating continuity of land and the prevalence of satisfactory conditions for the migration of plant life. The mountains of Chota Nagpur are assumed to have borne much the same flora as their extension into Assam and adjacent areas. These conditions are believed to have existed even up to Tertiary times, when a land connection between the Deccan plateau and the Indo-Malayan region was very probably in existence. 'The immediate result of the glacial epoch has been to eject the preglacial flora of the Himalaya to the south where there was sufficient warmth for it to exist. The retreat of the ice would see the return of the Indo-Malayan flora, the advance of which was facilitated by the mountainous country which lay to the south and south-east. If this theory be correct, one would expect to find a general resemblance in the floras of the Eastern Himalaya, the Khasia and the Naga Hills'. What part the Satpuras played in the geological upheavals, their antiquity and relationship in the formation of the Indo-gangetic plain is a question which so far as floristic studies are concerned cannot be answered satisfactorily in the present state of our knowledge of the systematics, ecology and phytogeography of the Central Indian and the neighbouring areas.

The affinities of different types of floras and the range of distribution of particular species, its ecology and antiquity have to be carefully studied and the results

should be correlated with the physical features, climatic and geological events responsible for the present configuration of the Indian Peninsula. It is needless to point out that every modification of climate, every disturbances of soil relations, every interference with the existing vegetation favours some species at the expense of others. And the whole vegetation is the result of continuous interaction of climatic, edaphic and biotic factors. Further, it is impossible to circumscribe the limit of any one type of vegetation, as in each area considerable overlapping and intermingling of species occurs. Unless a comparative statistical analysis of the components of vegetation of all the botanical areas is available which is possible only after a thorough survey of the little explored and unexplored regions of India, it is difficult to say anything definitely regarding questions connected with botanical geography.

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GEOGRAPHICAL FEATURES OF THE FLORA OF THE BAILADILA RANGE IN BASTAR STATE, C.P.

By SUNDER LAL HORA, *D.Sc., F.R.S.E., F.Z.S., F.R.A.S.B., F.N.I., Director, Zoological Survey of India, Indian Museum, Calcutta.*

BAILADILA RANGE AND THE AFFINITIES OF ITS FLORA.

While discussing the Satpura Hypothesis of the distribution of animals of Malayan affinities with Peninsular India, Mr. Salim Ali kindly directed my attention to Mooney's (1942) article entitled 'A Sketch of the Flora of the Bailadila Range in Bastar State'. It is a remarkable article for a study of the plant geography of the area and Mooney has attempted to explain his facts by advancing several hypotheses, which deserve careful consideration.

Bailadila lies between 18° 30′ and 19° 5′ north and 81° 10′ and 81° 15′ east and extends for some 45 miles south of the Indravati; both geographically and geologically it forms a separate unit. It rises sharply on all its aspects and reaches a height of over 3,000 feet for much of its length. Several peaks exceed 4,000 feet, the highest being 4,185. Though Bailadila lies more than a hundred miles west of the main chain of the Eastern Ghats, some of the intervening country consists of wooded hills running up to 3,000 feet, thus providing an avenue for the exchange of animal and plant life. Apart from this scanty connection, Bailadila is very isolated, the next high range of hills to the north being the Satpuras, over 300 miles distant, while to the west and south there are no mountains of comparable size until the Western Ghats and the Nilgiri Hills, well over 500 miles away, are reached.

From the standpoint of plant geography, Mooney has divided the total assemblage of plants into the following categories:—

(i) Plants having a northerly or north-easterly affinity.
(ii) Plants with an easterly affinity.
(iii) Plants with a southerly or nearly southerly distribution.
(iv) Plants with a westerly affinity.

From an analysis of the distribution lists, Mooney has concluded that 'thirty-six species have a definitely northerly or north-easterly affinity; while thirty plants are South Indian. Besides, two species belong to the Western Peninsula and two derive their origin from easterly sources, namely, from Burma and the Eastern Ghats.'

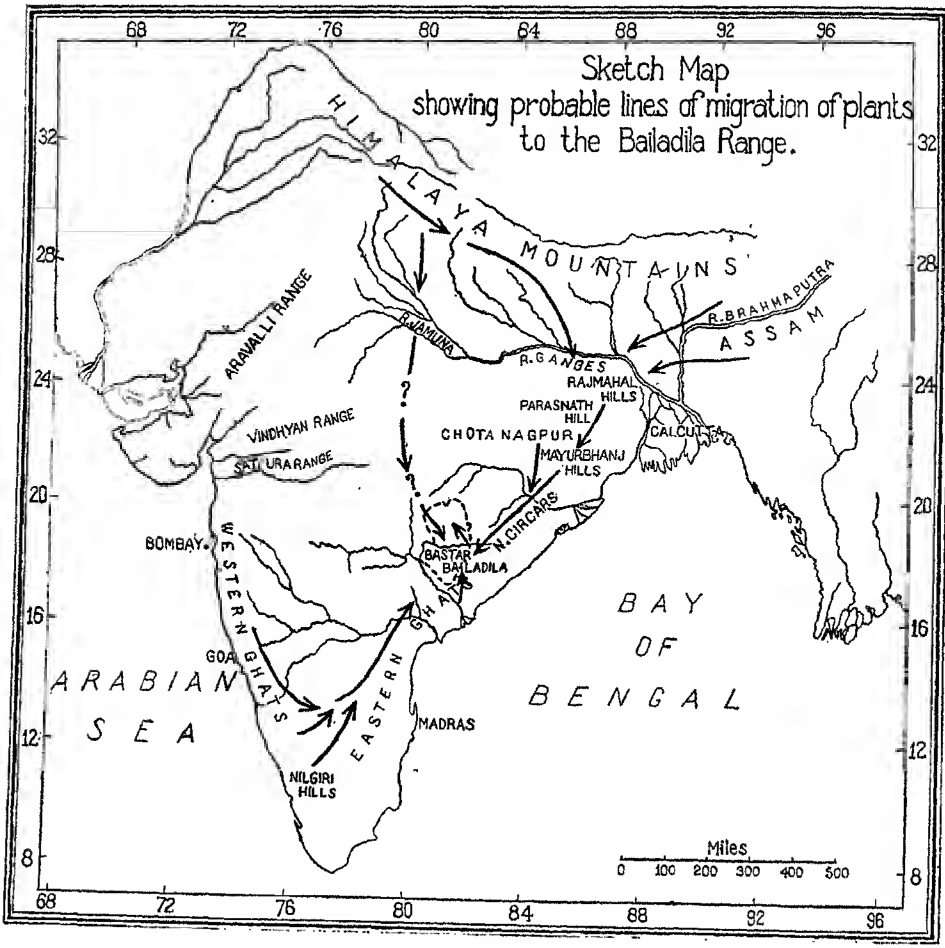
MOONEY'S VIEWS REGARDING THE PROBABLE ORIGIN OF THE BAILADILA FLORA.

Mooney has characterized the north-easterly influence interesting and stated that 'Its strength would seem to derive from the easy line of migration provided by the Rajmahal Hills, the highlands of Chota Nagpur, the mountains of Orissa and the hills of the Eastern Ghats, which terminate only some 100 miles or so east of Bailadila, and by the hills intervening between the Eastern Ghats and our area'. Thus he found this chain fairly continuous from Chota Nagpur southwards, and stated 'it is not a far cry from the Rajmahal Hills to the Bengal Duars and the hills of Sikkim and Assam. This provides a route by which plants could have migrated from Burma'. Though the present-day topographical and climatic conditions are not favourable for the plants and animals of the Assam Hills and the Eastern Himalayas to migrate to the Chota Nagpur Hills over the Rajmahal Hills, the Satpura Hypothesis of the writer postulates the existence of such favourable conditions over the intervening areas in the Pliocene and Pleistocene periods.

It may here be noted that, according to Mooney, it is not easy to explain how *Strobilanthes Falconeri* and *S. rufescens* reached Bailadila from Tenasserim and Pegu.

For the occurrence of the South Indian plants in the Bailadila Range, Mooney has postulated a hill-route and a river-route. As regards the hill-route he has stated:

> 'It does not call for great powers of imagination to visualize how species having their origin in the Nilgiris, Pulneys (*sic*), and other hills of Mysore, Travancore and Southern India may have travelled northwards along the line of the Eastern Ghats until they reached the northern extremity in the Kasipur plateau of Kalahandi State and the Agency Tracts of Ganjam and Vizagapatam districts with their humid coastal climate and many hills exceeding 4,000 feet in altitude. The distance from the southern plateau of Kalahandi to Bailadila in a straight line is not more than 120 miles; but Tulsi Dungri, itself 3,914 feet, situated about 50 miles east of Bailadila and other intermediate hill ranges of lesser calibre shorten the gap. Thus, the distance separating the northern end of the Eastern Ghats from our area is not much as to present any serious obstacle to transport by birds, animals or, in case of the lighter seed, by wind.'



As regards the river-route of dispersal of plants, Mooney has stated:

> 'The Indravati river provides a further route by which fruits and seeds may have been carried from the Kalahandi plateau to Bailadila. This river has its source in Thuamul-Rampur *zamindari* near Kasipur at a height of 3,100 feet and, after flowing through the

Jeypore Estate of Orissa, finds its way into Bastar and passes close to the northern extremity of the Bailadila range. Thus the connection between Bailadila and Southern India is fairly complete and the stretches of low ground are not such as to present a serious impediment to the dispersal of seed of the more readily transported and easily disseminated varieties of plants; and, given more favourable climatic and possibly physiographic conditions than those at present obtaining, the transit of plants would have been greatly facilitated.'

Mooney expressed great difficulty in explaining the dispersal of plants with northern and north-westerly affinity to Bailadila, but in dealing with the migration of high-level species from the Central Himalayas, most of which extending to the Eastern Himalayas, he thought that they followed the same route as the plants of the Assam Hills and the Bengal Duars. His map showing probable lines of migration of plants to the Bailadila Range summarizes his views on plants dispersal in an admirable way and this may be borne in mind for following the discussions.

Probable Age of the Bailadila Flora.

From a study of Mooney's paper, it appears that the endemic flora is almost insignificant. He found three new species belonging to the genera *Gymnosporia*, *Pygeum* and *Fimbristylis*. Only the first is named as *G. bailadilana* Narayanswami and Mooney, and is stated to approximate *G. Falconeri*. The other two species are not named in it, but regarding the new species of *Pygeum* it is stated that it is 'very like *P. Andersoni* Hook. f. in appearance, but differs in the glabrous petals and the larger number of stamens' (p. 223). *P. Andersoni* is listed by Mooney as occurring in the Bailadila Range and having northerly or north-easterly affinity. Regarding the Bailadila specimens referred by him to this species, he has observed (p. 225):

'If the identification is correct, this considerably extends the range of this rare species. It may, however, turn out to be an endemic species.'

Pygeum Andersoni has hitherto been known from Parasnath, Surguja and Mahendragiri.

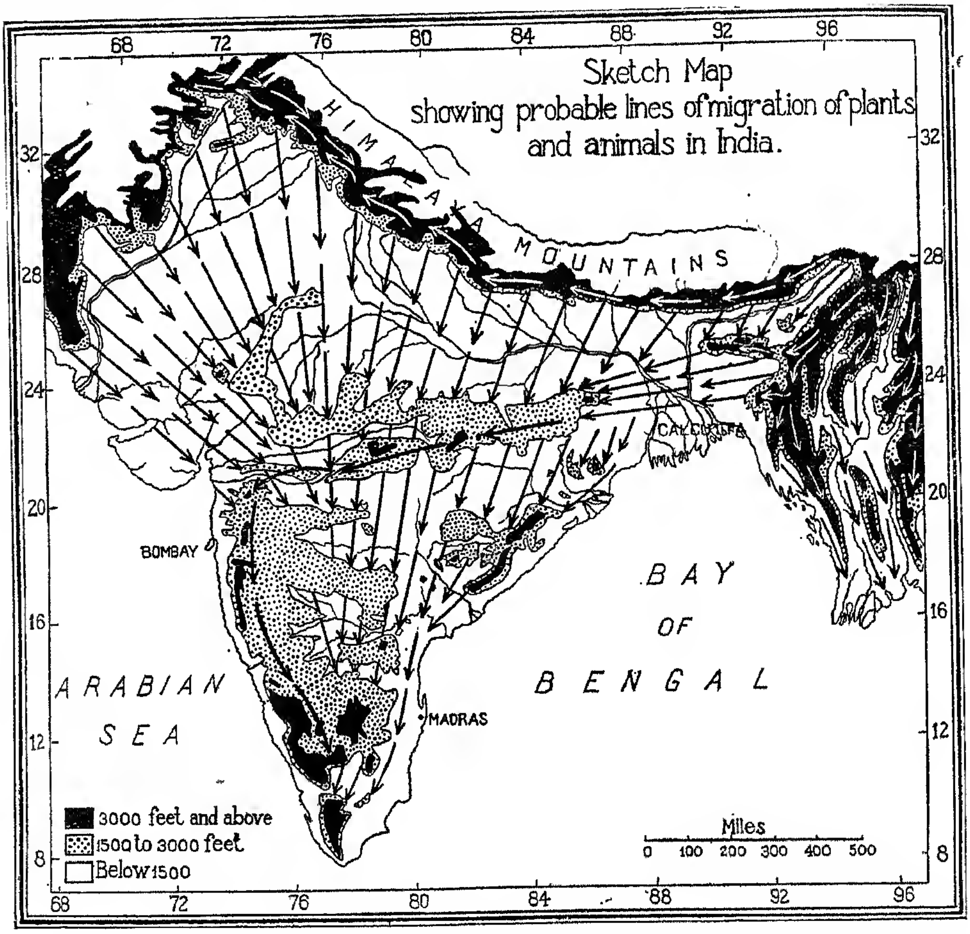
It will thus be seen that, since the isolation of the Bailadila flora, speciation has hardly proceeded even *One Species Step*. *Pygeum Andersoni* seems to be becoming polytypic in the Bailadila Range where two new forms can be differentiated from the *forma typica*. Even the new species of *Gymnosporia* approximates *G. Falconeri*. It will be of considerable interest if some botanist were to study in detail the intraspecific systematics of the Bailadila flora with a view to find out minor racial differentiations that may have occurred from the parent stock as a result of isolation.

From the above discussion, it is pertinent to infer that the special flora of the Bailadila Range migrated there during the Pleistocene, not more than a million years ago. I leave it for the botanist to dispute this view on the basis of speciation in the genera enumerated above.

Probable Origin of the Bailadila Flora.

Taking into consideration the probable age of the Bailadila flora as indicated above, it seems that dispersal must have taken place during the 'Pluvial Periods' when, as a result of glaciation in the Northern Hemisphere, the climates all over India were damper and more humid. Such favourable conditions for the dispersal of plants and terrestrial animals must have been more marked along hill ranges and must have lasted longer at higher altitudes, for they persist even today on the tops of isolated hills in Central and Southern India, and in humid situations along the Western and Eastern Ghats. As there is almost a continuous hill range from the Western Ghats to the Assam hills in the Vindhya-Satpura Trend of mountains, it

must have formed the most favourable route for the dispersal of both plants and terrestrial animals during these periods, and then along the almost continuous Western Ghats to Ceylon. Except at higher altitudes and in other suitable places, the moisture-loving flora and fauna must have died out during the 'Arid Periods' alternating with the 'Pluvial Periods'. As there were three Glacial Periods during the Pleistocene, the present-day flora of the Bailadila Range may be taken as the accumulative result of three distinct invasions and this would explain some of the anomalies in the distribution of plants and animals.



It seems to me unlikely that the flora of the Western Ghats and the Nilgiris could migrate north-eastwards to reach the Bailadila Range. Similarity in their flora could be accounted for on the assumption that this flora migrated from the north over a wide area under suitable conditions and now lies isolated in favourable situations, having died out from areas where the conditions became unfavourable for its existence. This applies equally to the faunas and floras of the Chota Nagpur and Satpura hills and those of the Aravalli range. In the accompanying map, I have indicated by arrows the probable routes of migration of plants and animals during the pluvial periods and it will be seen therefrom that the fauna and flora of Peninsular India possess all the three elements, north-easterly, middle

Himalayan and north-westerly. The north-easterly element is the most predominant owing to the continuity of mountain ranges and the consequent climatic factors characteristic of the Satpura Hypothesis.

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ADDENDUM.

When the above was in proof, the *Statesman* of December 4, 1949, reported the discovery of several plants of Malayan affinities in Madras. This item of news is reproduced below in full as it is relevant to the subject-matter of the Symposium and lends additional support to the views advanced in this article.

Discovery of Medicinal Plant in Madras.

NEW DELHI, Dec. 3.—A medicinal plant which is a reputed specific for black-water fever, has been discovered in the Rampa Agency tracts of Madras province as the result of botanical investigations undertaken by the Botanical Survey of India.

This plant, called *Vitax Peduncularis Var. Roxburghiana*, was formerly known to exist only in Assam. Examination of other collections brought from Rampa Agency has also revealed the existence of a number of plants originally growing in distant regions like the Himalayas, Assam, Burma and the Andaman Islands.—PTI.

DISCONTINUOUS DISTRIBUTION OF CERTAIN INDO-MALAYAN MAMMALS, AND ITS ZOOGEOGRAPHICAL SIGNIFICANCE.

By M. L. Roonwal and Bhola Nath, *Zoological Survey of India, Indian Museum, Calcutta.*

The fact that certain Malayan forms of mammals, and of other groups of animals, reappear in Peninsular India but are absent in the intervening tracts, has long been one of the puzzles of Indian zoogeography. Dr. Hora's Satpura Trend Theory would seem to provide a possible solution of this puzzle. It must, however, be mentioned that there are other attractive possibilities to explain the discontinuity. For instance, the migration path might lie along the Eastern Ghats. Or, similarity of environments in the two areas in question might be the cause of the independent origin of similar forms from an original common ancestral form. Or again, parallel evolution of the 'homologous series' type as propounded in Vavilov's Law (Vavilov, 1922), might be the cause of the evolution of similar evolutionary patterns in geographically distant genera and species. The present-day ecological similarity between the forest-types in Malaya, N. Burma and Assam on the one hand, and some of regions of the Western Ghats on the other, is striking. Dr. Hora's theory suggests that the intervening area, which he terms the Satpura Trend, was at one time a high, forested belt, continuous with the two areas mentioned above, and provided the pathway of migration. Ali (1948) has recently given a few examples from birds in support of the Satpura Theory. His map (p. 37), however, showing the Malayan forms migrating to India *via* N. Burma, does not appear to be well grounded, since all the evidence is in favour of S. China and N. Burma being the focus whence migration took place on the one hand towards India, and on the other towards Malaya.

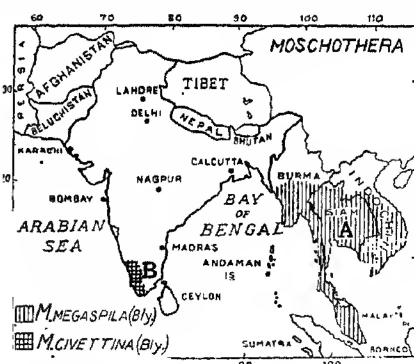
We shall give here three relevant examples from mammals. Two of these examples, namely *Charronia* and *Hemitragus*, have been quoted by Ali (1948) also.

Order CARNIVORA.

Family Viverridae.

Genus **Moschothera** Pocock (Text-fig. 1).

This genus is represented by two species, of which one, *M. megaspila* (Blyth), the large-spotted civet, is distributed in central and southern Burma, Malaya



Text-fig. 1.—Distribution of civets of the genus *Moschothera* Pocock. (A) *Moschothera megaspila* (Bly.), the Large-spotted Civet. (B) *Moschothera civettina* (Bly.), the Malabar Civet.

...onging to the family Megascolecidae under this genus are men-
tioned in the *Fauna* volume. The distribution of the genus is the Palni and Nilgiri

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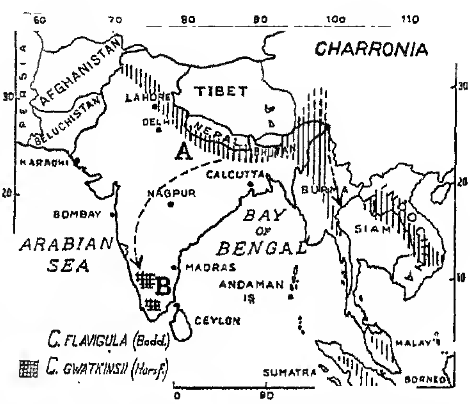
Peninsula, Siam and southern Indo-China. The other species, *M. civettina* (Blyth), the Malabar Civet, occurs in the coastal districts and W. Ghats of India. The two species are closely allied, and some authorities are even inclined to regard them as races of a single species. No representative of the genus occurs in the intervening tracts of India. Both species are jungle-inhabiting forms. The Malabar Civet is evidently on the wane. Formerly, according to Jerdon (1874), it was found from Malabar to Cape Comorin, including the forest-tracts of Wynaad, Coorg and Travancore. Recent collectors, however, do not appear to have met it, and the species is rare.

Family Mustelidae.

Genus **Charronia** Gray (Text-fig. 2). Marten

This genus of marten occurs in the whole of the Himalayan region and thence its distribution goes up to N. China and down to Siam, Malaya and some islands of the East Indies; it is absent in the whole of the remaining portion of India, except the higher ranges of the Nilgiris and Travancore. The Himalayan species is *C. flavigula* (Bodd.), the South Indian species *C. gwatkinsii* (Horsf.). Ali (1948) does not separate the latter species from the former. But an examination of the skins and skulls of the two forms makes it clear that they are specifically distinct (*vide* also Pocock, 1939).

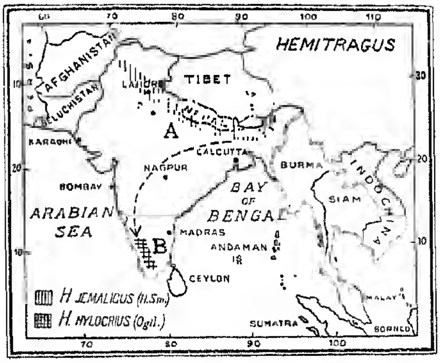


Text-fig. 2.—Distribution of martens of the genus *Charronia* Gray. Arrow indicates path of migration according to Dr. Hora's theory. (A) *Charronia navigula* (Bodd.); the N. Chinese range is not shown in the figure. (B) *Charronia gwatkinsii* (Horsf.).

Genus **Hemitragus** Hodgson (Text-fig. 3). Thar

This genus is represented in India by two species, *H. jemalicus* (Ham. Smith), the Himalayan Thar, and *H. hylocrius* (Ogil.), the Nilgiri Wild Goat. The former occurs throughout the Himalayas east up to Sikkim; the latter occurs in the W. Ghats. Between the distribution of these two forms, there is a wide gap where no representative of the genus occurs.

These three mammalian genera today show discontinuous distribution, but the two extreme limits of distribution were at one time presumably connected *via*, the 'Satpuras' along which, according to Dr. Hora's theory, distribution evidently occurred from the Assam-Burma end towards Peninsular India.



TEXT-FIG. 3.—Distribution of Indian species of the genus *Hemitragus* Hodgson. Arrow indicates path of migration according to Dr. Hora's theory. (A) *Hemitragus jemalicus* (Ham. Smith), the Himalayan Thar. (B) *Hemitragus hylocrius* (Ogil.), the Nilgiri Wild Goat.

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species belonging to the family ...ae under this genus are men-
tioned in the *Fauna* volume. The distribution of the genus is the Palni and Nilgir

THE SATPURA TREND AS AN ORNITHOGEOGRAPHICAL HIGHWAY.

By Salim Ali, *Bombay Natural History Society, Bombay.*

(Communicated by Dr. S. L. Hora, F.N.I.)

The significant fact of the occurrence in Ceylon and in the Travancore-Cochin-Malabar area (north to about Goa and Belgaum) of plant and animal forms not found elsewhere in peninsular India, either identical with or possessing close affinities with Indo-Chinese and Indo-Malayan forms, has been commented on by botanists and zoologists ever since systematic investigations were first undertaken in this country. Hooker and Thomson in their 'Introductory Essay to the Flora Indica' published in 1855 were perhaps the first to draw attention to the similarity in vegetation. Since then W. T. Blanford, A. R. Wallace and others have given numerous instances of animal forms exhibiting the same peculiarity.

In a previous paper (Salim Ali, 1935), I had occasion to dwell at some length on the Malayan element in the avifauna of the Travancore-Cochin area. Whistler (1944) brings to date the findings of older workers concerning the island of Ceylon, and recently (Salim Ali, 1948), I have succeeded by systematic collecting from the northernmost extremity of the Sahyadris or Western Ghats south of the Narbada (which dovetails into the western extremity of the Satpuras) to trace some significant extensions of range of a number of the peculiar forms of birds hitherto considered as more or less restricted to the Malabar Zone.

Biologists are generally agreed that the presence today of all these closely allied forms in such far flung discontinuous areas is accountable only on the presumption that these areas were at some past epoch directly connected with one another—not necessarily contemporaneously—and through their uniform physiography afforded continuity of those humid conditions and heavy rainfall which we find essential for the prevalence of these specialized forms. Of the two or three possibilities suggested as to the manner in which the geographical continuity in the distribution of plants and animals may have existed, the one that appeals most strongly from the ornithological point of view is that suggested and so ably developed by Dr. S. L. Hora. This hypothesis postulates that from an original centre of distribution in the Szetschwan-Yunnan area, animals and plants spread to Malaysia over the southern arm of the newly upraised Himalayan trend—the mountain ranges of Assam, Arakan and Tenasserim, continuing into Malaysia—and westward over the Eastern Himalayas across a mountain connection, since lost, over the Garo-Rajmahal hills gap (or alternatively between Darjeeling and Monghyr), then over the Satpura trend of mountains across the peninsula to the Western Ghats and southward along that trend to Cape Comorin and Ceylon. Taking into account the comparative youthfulness of the Himalayas in relation to the mountains of Yunnan that abut on them, and a critical study of the present-day distribution of Indo-Chinese and Indo-Malayan avifauna, it can scarcely be doubted that most East Himalayan and Malaysian forms have been derived from the region of Yunnan.

The plausibility of Dr. Hora's hypothesis is heightened by his own studies of the fish fauna inhabiting torrential streams of the area covered by what has aptly been termed this zoogeographical 'horseshoe' whose eastern terminal is Malaysia and western Ceylon. The physiology of torrential fishes is shown to be so closely adapted to the special conditions under which they live that there seems no way in which they could have attained their present far-flung discontinuous distribution

unless there was at some time or other a direct connection between the hill streams they inhabit.

Details will be found in Dr. Hora's contribution to this symposium, and contributors on other classes of animal life and plants will doubtless furnish what evidence they possess for or against this interesting hypothesis. Without going into detail or discussing any of the alternative suggestions regarding the route by which eastern forms may have reached peninsular India and Ceylon, I would like to put forward such ornithological evidence as we are able to adduce, all of which in my opinion lend significant support to the postulate of the Satpuras having been the highway of their westward spread.

It must be made clear, however, that our knowledge of the ornithology of the Satpura and Vindhya mountains, as well as that of the Aravallis, is as yet very incomplete and defective. Throughout the length of the Satpura trend there are no doubt many 'pockets' or 'islands' lying at elevations over 3,500 ft.—similar to Pachmarhi or Parasnath Hill—with the requisite rainfall and humidity for producing the biotopes essential for the survival of the specialized forms that concern the present enquiry. A systematic investigation of such isolated patches of evergreen or moist deciduous forest would provide evidence of the greatest value: it is a subject that deserves high priority on the field programme of the Zoological Survey of India.

Numerous genera and species of birds can be cited occurring in Ceylon and the Malabar zone of south-western India whose nearest relatives are to be found only in the Indo-Chinese countries, the Eastern Himalayas and southward to Malaysia. The following are some of the more outstanding examples and will suffice for our present purpose. I feel confident that a closer investigation of suitable isolated biotopes along the Satpura trend will reveal further 'milestones' in the distributional journey of some of these forms, and much other evidence bearing on the question.

Genus **Garrulax** Lesson.

(Laughing Thrushes.)

(Forest-frequenting birds of evergreen biotope found from the level of the plains up to about 9,000 ft. elevation, but usually to 4,500 feet, varying with locality and species.)

Represented along the Himalayan trend (i.e. including Pakistan and Burma) by 6 species in at least 12 geographic races, from the Hazara country in the west to North Chin and Kachin Hills on the east; Assam, Cachar, Shan States, Central Burma, Pegu and Tenasserim. Extralimital, the genus occurs in Yunnan, Hainan, Thailand, Annam, Cambodia, Malaysia.

One isolated species, *Garrulax delesserti* (Jerdon), is confined to the Malabar zone (Wynaad to South Travancore) while Ceylon possesses another, *G. cinereifrons* Blyth. The distance separating *G. delesserti* from its nearest northern congener is 1,000 miles, and across the Bay of Bengal 1,500 miles.

Genus **Trochalopteron** Blyth.

(Laughing Thrushes.)

(Forest-frequenting birds of evergreen biotope found at elevations of over about 4,000 ft.)

Represented along the Himalayan trend by about 11 species in some 27 races; from the Afghan frontier in the west to the Mishmi Hills in the east, and beyond into Yunnan, etc., eastward the genus extends to Eastern China; southward to Malaysia. (See map.)

Two isolated species occur in the Malabar zone of South India, viz. *Trochalopteron cachinnans* (Jerdon) and *T. jerdoni* (Blyth), the latter in 2 races. Their range is almost exactly coincident with that of the Nilgiri Tahr. The genus is absent in Ceylon.

Genus **Oreocincla** Gould.

(Mountain Thrushes.)

(Inhabits hill forests and sholas usually between 2,000 and 4,000 ft. elevation. Often considerably higher in the Himalayas.)

Represented along the Himalayan trend by 3 species in 5 races from the Afghan frontier in the west to the Mishmi Hills in the east. Extra-limital, it is found in Yunnan and farther east; Annam, Thailand, Malaysia, etc.

A race of the Himalayan species *dauma* (*neilgherriensis*) Blyth is found in the Malabar zone of S. India. A second race *imbricata* (Layard) is peculiar to Ceylon, while that island also possesses an endemic species *O. spiloptera* Blyth.

Genus **Irena** Horsjfield.

(The Fairy Bluebird.)

(One species *Irena puella* (Latham) is an inhabitant of evergreen biotope from almost plains level to about 4,000 ft. elevation.)

Distribution: Eastern Himalayas from Sikkim and Bhutan to the Mishmi Hills. East to Yunnan, Annam, Cochin-China; south through Burma, Thailand and Tenasserim to Malaysia; Andamans and Nicobars. Also the Malabar zone of S. India and Chitteri Hills (possibly also the Shevaroys), separated by a break of at least 1,200 miles from the East-Himalayan population. It is rare (straggler ?) in Ceylon.

The Fauna of British India series on birds (Vol. iii, p. 2) gives its breeding range as from Travancore to Kanara and Khandesh. The basis for the inclusion of Khandesh is unknown since the claim is unsupported by reliable evidence. The most northerly authentic record so far is from Savantvadi near Goa. Nevertheless, I feel that a careful investigation of how far north in the Ghats this species extends, and whether along the Satpuras or to the Chota Nagpur-Rajmahal Hills area needs to be undertaken.

Genus **Arachnothera** Temm. and Laug.

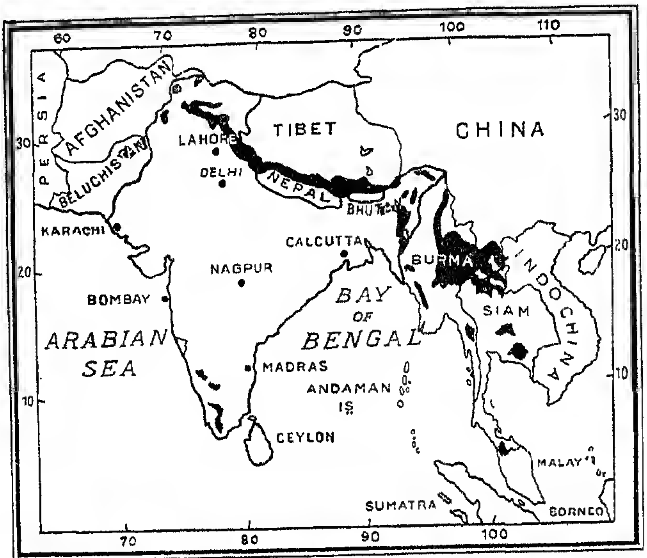
(Spider Hunters.)

(Birds of tropical and sub-tropical rain forest.)

Represented along the Himalayan trend by 4 species in 5 races from Sutlej Valley to the Mishmi Hills. Extra-limital in Yunnan, Thailand, Annam, Cochin-China, etc., and south to Malaysia.

The distribution of one species and race, *A. longirostris longirostris* (Latham) is remarkable. It occurs in eastern and southern Assam, E. Bengal (Tipperah), Chittagong, the hill tracts from Manipur to the Chin Hills; Burma, Shan States, Thailand, Annam, Cochin-China and Malaysia.

After a break of over 1,000 miles from its nearest inhabited area, the same species and race reappears in the Malabar zone of S.W. India. It does not occur in Ceylon.



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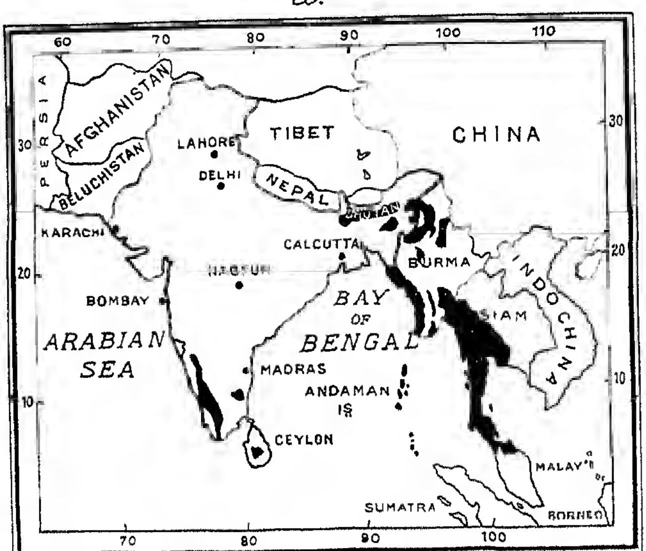


b.

FIG. 1*a*. The distribution of the genus *Trochalopteron* (Laughing Thrushes) in India, Pakistan and Burma.

FIG. 1*b*. The distribution of the Fairy Bluebird (*Irena puella*) in Ceylon, India and Burma.

Genus **Hemicircus** Swainson.

Hemicircus canente (Lesson): The Heart-spotted Woodpecker.

(Inhabitant of moist deciduous or semi-evergreen biotope.)

The typical race *canente* (Lesson) occurs in Assam, Burma, Thailand, Annam, Cochin-China and Malaysia.

A second race *cordatus* Jerdon—somewhat smaller in size with a smaller bill—was hitherto believed to be confined to the Malabar zone of S.W. India. Seventy years ago Jerdon had recorded it from the 'Chanda forest' in the Central Provinces, but since then it had apparently been lost sight of there. Within the last 10 years, however, it was authentically recorded for the first time in the wooded hills of the Tulsi Lake catchment area in Greater Bombay. The recent Gujarat ornithological survey extended its range still further north to the northern extremity of the W. Ghats, having procured specimens in its typical biotope in the Songadh forests of Navsari Prant, south of the Tapti River. The possibility of its occurrence along the Satpuras and in the Chota-Nagpur-Rajmahal Hills area needs to be investigated.

Genus **Dryocopus** Wied.

Dryocopus javensis (Horsf.): The Great Black Woodpecker.

(Inhabitant of moist deciduous or semi-evergreen biotope.)

The typical race of this woodpecker *D.j. javensis* (Horsf.) and two others are found in Malaysia. A fourth race *D.j. feddeni* (Blyth.) occurs in Burma, north to the Chin Hills so far as is known at present. A fifth race *D.j. hodgsoni* (Jerdon) was until recently considered as restricted to the Malabar zone, the northernmost record according to Stuart Baker (*Fauna*, iv, 90) being from Belgaum. The Gujarat Ornithological Survey recently extended its limit northward along the Ghats to the Tapti River, to the intermingling zone of forested foothills of the Western Ghats and the Satpuras. It is confidently expected that careful investigation will bring to light its presence in the appropriate biotope along the Satpuras and also in the Chota Nagpur-Rajmahals area, thus providing evidence of the route by which it travelled westward.

Genus **Vivia** Hodgson.

Vivia innominatus (Burton): The Speckled Piculet.

(Inhabitant of evergreen and most deciduous biotope.)

This tiny woodpecker in two races occurs along the Himalayan trend from Dharmsala in the west to Assam (Mishmi Hills ?) and south to Tenasserim. Extra-limital it is found in Thailand, Annam, etc., and Malaysia.

A third race *V.i. avunculorum* Hartert inhabits the Malabar zone of S.W. India, as far north as the Sirsi taluka of North Kanara according to present knowledge.

Genus **Alcemerops** Geoff.

Alcemerops athertoni (Jardine and Selby): The Blue-bearded Bee-eater.

(Inhabitant of evergreen and moist deciduous biotope up to about 5,000 ft. elevation.)

Occurs in the Himalayas from about Dehra Dun in the west to East and Southern Assam, East Bengal, Chittagong, Vizagapatam Ghats. Extra-limital, in Thailand.

In peninsular India according to Stuart Baker (*Fauna*, iv, 242) it is confined to the west coast from Travancore to Belgaum, and also recorded as occurring in Sambalpur. On the western side, the recent Gujarat ornithological survey extended the northern limit of its distribution to the Tapti River, and I have an undoubted aural record of it from Rajpipla territory just south of the Narbada. Its discovery in the area of the Gujarat Satpuras is of interest because within the last few years it has also been recorded at and around Pachmarhi a more easterly station along the same trend, thus providing an additional milestone to Sambalpur on the postulated highway of East-Himalayan forms to the Malabar zone. This bee-eater does not occur in Ceylon.

Genus **Dichoceros** Gloger.

Dichoceros bicornis (Linn.): The Great Indian Hornbill.

(Inhabitant of tropical and sub-tropical rain forests of South-East Asia.)

Distributed along the Himalayan trend from Kumaon in the west to Mishmi Hills on the east; south to Tenasserim. Extra-limital in Thailand and Malaysia.

Also occurs in the Malabar zone of S.W. India separated from the rest of its range by at least 1,000 miles of intervening country. It is absent in Ceylon.

Genus **Lyncornis** Gould.

Lyncornis cerviniceps Gould: The Great Eared Nightjar.

(Birds of evergreen biotope; lower hill forest, usually under 3,000 ft. elevation.)

Represented by the typical race *L.c. cerviniceps* Gould in Eastern Bengal and Assam, Burma, Thailand and Malaysia. Various geographical races of this as well as of an allied species are found right up to New Guinea.

One race of *L. cerviniceps*, viz. *bourdilloni* Hume is confined to Travancore, the northernmost point at which it has so far been found being Thattakad ca 10° 7′N. latitude.

Genus **Batrachostomus** Gould.

(Frogmouths.)

(Birds of evergreen biotope, belonging to the family Podargidae found over the greater part of the Australasian Region.)

Represented by two species in the Eastern Himalayas from Sikkim to the Mishmi Hills; Assam, Burma, Thailand, Malaysia, etc.

A third species, *B. moniliger* Blyth, occurs in Ceylon and the Malabar zone of S.W. India.

Genus **Tephrodornis** Swainson.

Tephrodornis gularis (Raffles): The Large Wood-Shrike.

(Inhabitant of evergreen or moist deciduous biotope.)

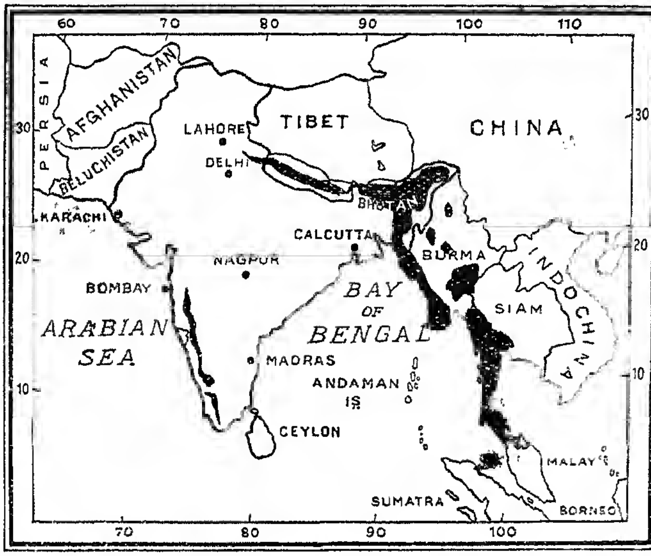
The race *pelvica* (Hodgs.) according to the *Fauna* (ii, 310) occurs in the Himalayas from Nepal to Eastern Assam; practically all Burma; the northern parts of the Malay Peninsula; Shan States, Yunnan, Thailand and Cochin-China. Other races occur in Malaysia.

Represented in Western India by the race *sylvicola* (Jerdon) whose distribution the *Fauna* gives as follows: 'The West Coast of India from the extreme south almost to Bombay City; Nilgiris and adjoining hills, Nelliampathy Hills, etc., up to nearly 6,000 ft.'

The limit of *sylvicola* has been extended considerably farther north by the recent Gujarat Ornithological Survey which collected a specimen at Waghai in the Surat Dangs. Although it was said to be found 'almost to Bombay City' the most northerly authentic record that could hitherto be traced had only been Belgaum.

The East-Himalayan race *pelvica* has recently been procured in the Vizagapatam Ghats, but the species is so far unrecorded from anywhere along the Satpura trend or from the Chota Nagpur-Rajmahal Hills area. Careful field work will doubtless reveal its presence in suitable biotope there.

Besides the above, numerous other examples could be cited from almost every endemic bird family which exhibit the same peculiarities of discontinuous distri-



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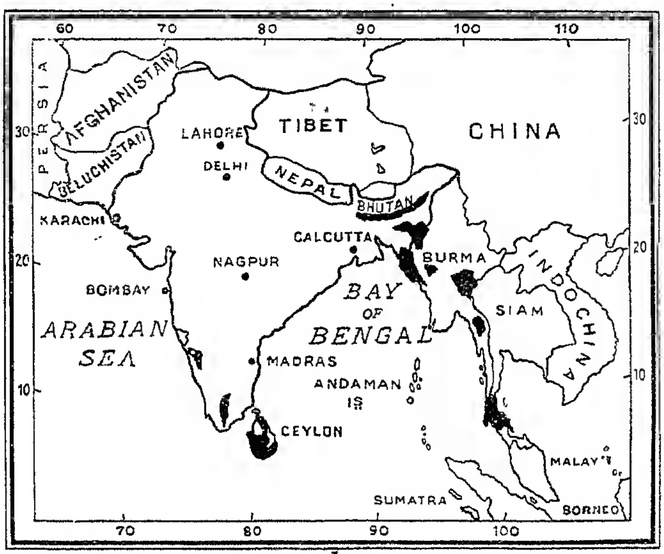

b.

FIG. 2*a*. The distribution of the Great Hornbill (*Dichoceros bicornis*) in India and Burma.

FIG. 2*b*. The distribution of the genus *Batrachostomus* (Frogmouths) in Ceylon, India and Burma.

bution in a greater or lesser degree. Some of them are:—*Hemipus picatus* (Sykes), *Pericrocotus flammeus* (Forster), *Aethopyga siparaja* (Raffles), *Eurystomus orientalis* (Linn.), *Hirundapus giganteus* (Temm. and Laug.), *Chrysocolaptes guttacristatus* (Tickell), *Dinopium javanense* (Ljung.), *Alcedo meninting* Horsf. *Ceyx tridactylus* (Pallas), *Harpactes fasciatus* (Pennant), *Huhua nipalensis* Hodgs., *Baza leuphotes* (Dumont), *Baza jerdoni* (Blyth), *Lophotriorchis kieneri* (de Sparre), *Ducula badia* (Raffles) and *Gorsakius melanolophus* (Raffles).

There are two records in the literature which have hitherto been looked upon with suspicion, but which in the light of recent findings need careful re-examination. A specimen of the Southern Tree-Pie (*Dendrocitta leucogastra* Gould was recorded by McMaster from the Gawilgarh Hills near Chikalda, Amraoti District, Berar) about 80 years ago, and also the Black Bulbul (*Microscelis psaroides* (Vigors)). These records have not since been repeated. Stuart Baker (*Fauna*, i, 52) disposes of the former by saying 'apparently a straggler only'. But in the case of so sedentary a species whose known distribution at present is restricted to the Malabar zone (Southern India from South Travancore to the Wynaad) it is not easy to understand why or how it could have straggled so far north-east. Since the Gawilgarh Hills record is authentic and supported by a skin, it does not seem unreasonable to suggest that it may represent a population that is now either extinct, or that the species may still be tucked away in some isolated pockets of the requisite humid evergreen biotope at remote points along the Satpuras, possibly extending eastward into the Bastar, Chota Nagpur and Rajmahal Hills areas. Should this prove to be the case, it will be worth while to examine more closely and determine the true taxonomical relationship between this species and the Brown-browed Tree-Pie (*D. frontalis* Horsfield) of the Eastern Himalayas, Assam, and North Burma hills.

As regards *Microscelis psaroides*, the known range of this bulbul at present is from Ceylon through the South Indian hills northward along the Western Ghats to about Matheran. The only other area whence it has been recorded in the peninsula is the Shevaroy Hills. In the Himalayas this species occurs west to east, to the Mishmi Hills and beyond in Yunnan. It is also found in Burma, Thailand, Tenasserim and Malaysia, in evergreen and moist deciduous biotope, breeding mostly in the hills between 2,000 and 8,000 ft. elevation. That here again the spread to peninsular India has been along the Satpura trend seems more than likely. The point needs to be cleared up by careful collecting.

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SOME PECULIARITIES OF AVIFAUNAL DISTRIBUTION IN PENINSULAR INDIA.

By HUMAYUN ABDULALI.

(Communicated by Dr. S. L. Hora, F.N.I.)

When in a moment of enthusiasm I promised Dr. Hora to try and make an ornithological contribution to the Symposium on the Satpura Theory of floral and faunal distribution in Peninsular India, I did not have a very clear idea of what I would do. As a matter of fact, Salim Ali in his several papers has already dealt with the ornithological sidelights and I have only tried to place the south-west forms (so far known as Indo-Malayan species) into different groups based on their present distribution which may give us an indication of the time when they were cut off from their original source and also to show which way they may have come. I have not been able to follow this grouping to its logical conclusion, i.e., by establishing the relationships of the various species outside India but I offer these lists as the basis for further work in this connection.

Whistler in his Avifaunal Survey of Ceylon has dealt at some length with the 22 forms peculiar to that island and decided that the avifaunal relations are more with India than with Malaya.

In the Andamans, migrants, which do not come into Peninsular India, like:—

Phylloscopus fuscatus	*Turdus obscura*
Pericrocotus cinereus	*Emberiza pusilla* and *aureola*, and
Agropsar sturninus	*Anthus cervinus*

together with several resident forms of Parakeets, Pigeons, Collocalias and Cuckoo-doves, indicate closer affinities with Burma.

For peninsular India, south of the Garo-Rajmahal gap, my first group is of 'South West' forms which are restricted to the west coast of India and whose distribution does not, as at present known, link up with the Rajmahal section of the Garo-Rajmahal Gap.

It should, however, be mentioned that all these forms are not peculiar to the South-West, but are of Indo-Malayan or of Indo-Chinese origin, some of them having affinities even in the Western Himalayas.

(The northernmost point of occurrence is indicated against each species. An asterisk on the left indicates its occurrence in Ceylon as well, and one on the right, in the Andamans.)

LIST I.

Species.	Northern Limit of Distribution along Western Ghats. (Occurrences in the South-Eastern Ghats are in brackets.)
Pycnonotus xantholaemus	Malabar (Chitteri Range and Horsleykonda).
Trochalopteron jerdoni	(three races).
Trochalopteron cachinans	(two races).
Brachypteryx major ..	(two races).
Eumiyas albicaudata ..	
Ochromela nigrorufa ..	
Schoenicola platyura ..	
Hirundo javanica ..	
Anthus nilghiriensis ..	
Eurystomus orientalis	

Species.	Northern Limit of Distribution along Western Ghats. (Occurrences in the South-Eastern Ghats are in brackets.)
Lyncornis macrotis	Malabar (Chitteri Range and Horsleykonda).
*_Nisaetus nipalensis_	
*_Baza jerdoni_	,,
Dendrocitta leucogastra	North Kanara (McMaster in Gawilgarh Hills?).
Garrulax delesserti	,,
Argya subrufa	,, (Shevaroys).
*_Rhopocichla atriceps_	,,
Pycnonotus gularis	,,
Microtarsus poiocephalus	,,
Muscicapula pallipes	,, (nearest subspecies in China).
Arachnothera longirostra	,,
*_Picus xanthopygaeus_	North Kanara (Central India).
Dinopium javanense	
*_Xantholoema rubricapilla_	
Centropus bengalensis	
*_Alcedo meninting_*	
Micropus pacificus leuconyx	North Kanara only.
*_Chaetura giganteus_*	North Kanara.
*_Batrachostomus moniliger_	,,
Huhua nipalensis	,, (Shevaroys).
*_Irena puella_*	Sawantwadi.
_Dicaeum concolor_*	South Konkan.
_Sauropatis chloris_*	South Konkan only.
*_Collocalia fuciphaga_	South Konkan.
*_Microscelis psaroides_	Matheran and Khandalla (McMaster in Gawilgarh Hills ?).
*_Iole icterica_	Khandalla.
Sturnia malabarica blythii	Bombay.
Aethiopsar fuscus	Bombay-Khandalla (Shevaroys and Chitteri Range).
*_Munia malacca_*	Khandalla, Pachmarhi (Pakhal Lake, East Hyderabad; Kolair Lake between Godavari and Krishna).
*_Cinnyris lotenia_	Bombay (Nallamalai Hills, Chingleput, Madras).
Cinnyris minima	Bombay-Khandalla.
Psittacula columboides	
*_Ceyx erithaca_*	
Dichoceros bicornis	Mahableshwar
Tockus griseus	Bombay-Khandalla
Falco tinnunculus objurgatus	Bombay-Mahableshwar-Matheran (Shevaroys).
*_Accipiter virgatus besra_	Bombay.
*_Dendrophassa pompadora_	,,
Columba elphinstoni	Matheran-South Hyderabad.
Hemicircus canente	Dangs.
Macropicus javensis	,,
Thereiceryx viridis	,, (Shevaroys, Chitteri Range).

It will be noticed that of the 52 species extending along the West Coast up to North Kanara, Bombay or the Dangs, 19 occur in Ceylon and 9 in the Andamans. These 9 include 7 which are common to Ceylon. Special attention might be drawn

to *Sauropatis chloris* which has been recorded from a small area in the South Konkan and is then found in the Andamans.

List II.

We then have another list of 27 of the 'South West' forms which extend north to North Kanara, Bombay and the Dangs, usually much further than those on the first list but which occur again south of the Garo-Rajmahal Gap, i.e., in North C.P., North-Eastern Ghats and/or Chota Nagpur. 14 of these 27 species occur in Ceylon and 5 in the Andamans (including 3 common with Ceylon). The asterisk on the left indicates its occurrence in Ceylon and on the right, in the Andamans:

Species.	Northern Limit of Distribution in Western Ghats followed by records from other places in Peninsular India south of Garo-Rajmahal Gap.
Cisticola exilis	Malabar, Saugor in C.P., Kumaon.
**Astur trivirgatus*	,, Balaghat, Vizagapatam Hills.
**Dendrophassa bicincta* ..	,, ,, ,,
**Excalfactoria chinensis*	,, East Hyderabad, Chota Nagpur, (Bhopal, Central India).
**Oreocincla dauma* ..	N. Kanara, Chota Nagpur.
Vivia innominatus ..	N. Kanara, Vizagapatam Hills.
**Rhopodytes viridirostris*	N. Kanara, Vizagapatam Hills, (Chitteri Range, Nallamallais, Ellore).
Merops leschenaulti ..	N. Kanara, East Hyderabad State, Chota Nagpur (Shevaroys).
Alcemerops athertoni ..	N. Kanara, Pachmarhi, Vizagapatam Hills, (Chitteri and Shevaroys).
Indicapus sylvaticus ..	N. Kanara, Raipur, Seoni in C.P., Sambalpur.
**Lophotriorchis kinnerii*	,, Chaibassa.
Ducula badia ..	,, Vizagapatam Hills.
Cryptoplectron erythrorhynchum	,, Chanda and Sironcha in C.P., Vizagapatam Hills.
Chibia hottentotta ..	S. Konkan, Chota Nagpur.
**Hydrocissa coronata* ..	,, ,, (Gumsoor in Ganjam).
Chaptia aenea ..	Bombay-Khandalla, Vizagapatam Hills (Shevaroys, Chitteri Hills, Bastar).
Gracula religiosa ..	Bombay, Sambalpur and Goomsoor.
*Coryllis vernalis** ..	Bombay-Khandalla, Vizagapatam Hills.
**Ictinaetus malayensis* ..	Bombay-Mahableshwar, Pachmarhi area C.P., Bastar, Vizagapatam Hills.
Muscadivora aenea ..	Bombay, East and South Hyderabad, Chota Nagpur (Chitteri, Palkonda, Nellore, Jeypore).
**Hemipus picatus* ..	Patchily throughout Western Ghats, C.P. and then in Vizagapatam Hills.
*Tephrodornis gularis**	North Kanara, Dangs, Vizagapatam.
*Aethopyga siparaja** ..	,, ,, Rajmahal Hills.
Chrysocolaptes guttacristatus	,, ,, Vizagapatam Hills.
**Harpactes fasciatus* ..	Dangs, Khandesh, Vizagapatam Hills, Chota Nagpur (N. of Ellore).
Caprimulgus macrourus	North Kanara, Dangs, Gawilgarh Hills, Balaghat, Vizagapatam Hills.
Ninox scutulata ..	Dangs, Chota Nagpur.

It will be noticed that in some species there appears to be a gap in distribution between North Kanara and the Dangs, i.e., they are absent from the South Konkan and Bombay. There is then a very appreciable gap in our knowledge of their distribution between the northern extremity of the Western Ghats and the hills south of Rajmahal Hills.

Mr. Salim Ali has expressed the opinion that further research along the Satpuras in Central India would lead to many of these species being linked up in their distribution. Personally, I think that there is an alternative possibility of the species having reached South-West India through the Eastern Ghats. Our knowledge of the natural history of the Eastern Ghats is much scantier than that of the West. Few people have done any serious collecting and most of the information that is available from that area is in the form of fragmentary notes. On south of the Rajmahal Hills, the Chota Nagpur area is common to both the Satpura route and one southward through the Vizagapatam Ghats. The data from the Vizagapatam Ghats form an important part of List No. II and also support the opinion that the migration moved southwards in this direction. Bastar State which holds many ornithological and other natural history secrets is also in this direction. Mahendragiri in the Northern Circars and the Nallamallai and other Hills which go to form the Eastern Ghats have not been carefully worked and it is quite possible that they may have been an important highway to Malabar and Ceylon. It is of course possible that this area merely forms a *cul-de-sac* southwards and is of no further significance.

The Eastern Ghats also appear to form an important route for some migrant forms which are known from the Malabar area but have not been recorded in the strip of Western Ghats farther north.

List III.

The following are partial to evergreen biotope and the evidence indicated against each of them shows that they now use, as they have presumably always done in the past, the Eastern Ghats highway:—

**Tarsiger brunnea* .	North Kanara, Malabar, Manbhum and Vizagapatam Hills (common).
**Geokichla wardii* .	Mysore, Vizagapatam Hills.
Lalage melaschista .	North Kanara, Gumsoor, Chota Nagpur.
Muscicapula superciliaris .	North Kanara, Mysore, Narsampet in East Hyderabad, (Bhopal and Gwalior), Vizagapatam Hills.
**Muscicapula rubeculoides* .	Malabar, North Kanara, Nallamallais, Vizagapatam Hills.
Alseonax ruficauda .	Malabar, S. Kanara, Nellore.
**Alseonax muttui* .	Travancore, N. Kanara, Secunderabad, S. Hyderabad (Nallamallais).
Hvmochlamys p. pallidipes.	Vizagapatam Hills.
**Oriolus chinensis* .	Malabar, North Kanara, Vizagapatam.
Clamator coromandus .	Ceylon, Malabar (regular visitor), North Kanara, Bombay, South Konkan (Straggler), Carnatic, Madras.
**Baza leuphotes*	Travancore, Pondicherry, Trichinopoly, Nellore.
**Scolopax rusticola*	Malabar, Nilgiris, N. Kanara, Shevaroys and Jevadi Hills, Vizagapatam Hills.

List IV.

There are some more winter visitors to extreme South India chiefly from the Eastern Himalayas and whose line of migration appears to follow the Eastern Ghat route:—

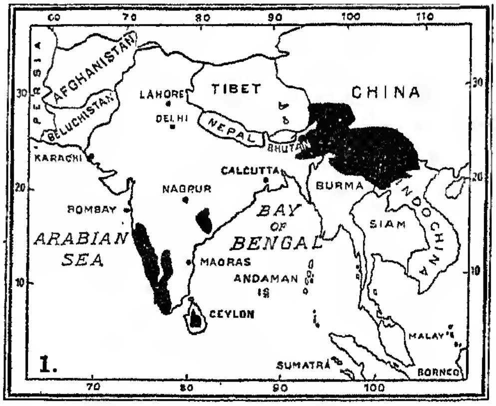
Calliope calliope	North Kanara, Bombay (Straggler), Vizagapatam Hills (common).
Turdus unicolor	Chota Nagpur to Raipur and Vizagapatam Hills.
**Geokichla citrina*	Gumsoor, Chingleput, Chota Nagpur.
*Lanius c. cristatus**	Malabar and North Kanara, Hyderabad State, Seshachalam and Nallamallai Hills (common in Andamans).
**Lanius cristatus luscionensis*	Travancore (once), common in Andamans.
*Phargmaticola aedon** ..	Malabar, Nellore, Vizagapatam Hills.
Phylloscopus proregulus ..	Chota Nagpur.
Seicerus burkii whistleri ..	Vizagapatam Hills.
Locustella certhiola ..	Ceylon and Andamans.
Anthus hodgsoni ..	Malabar, N. Kanara, Balaghat, Godavery Delta.
Chalcites xanthorhynchus ..	Madras.
Chalcites maculatus ..	Madras (Straggler).
**Falco severus*	Malabar.
**Erythropus amurensis* ..	N. Kanara, Carnatic, Nellore, Rajahmundry.
**F. t. interstinctus* ..	Coimbatore
**Circus melanoleucus* ..	Malabar, N. Kanara, Bombay (rare), Balaghat, Chingleput, Vizagapatam Hills (common).

List V.

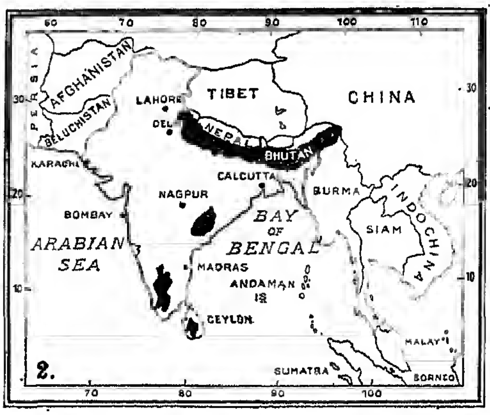
The last list is of resident forms which have been found south of the gap but which do not appear to have penetrated far into Peninsular India. Where their ranges have been extended further southwards, it will be found that the Eastern Ghats theory is supported. It will be noticed that *Mixornis gularis rubricapilla* goes right down into Mysore. The status of *Tyto longimembris* is doubtful as there is no record of its breeding in this area and it may possibly be a migrant:—

Dendrocitta formosae	Mahendragiri, Vizagapatam Hills. Jerdon got a specimen killed in the Eastern Ghats and Horsfield also had one from Madras.
Stachyridopsis rufifrons ambigua	Vizagapatam Hills.
Mixornis gularis rubricapilla	Chota Nagpur, Vizagapatam Hills, Bastar, Mysore.
Otocompsa flaviventris ..	Chota Nagpur, Vizagapatam Hills (South of Pachmarhi).
Leucocirca albicollis ..	Chota Nagpur
Muscicapula poliogenys vernayi	Vizagapatam Hills.
Lanius nasutus nigriceps ..	Chota Nagpur, Vizagapatam Hills.
Tyto longimembris ..	Nilgiris and Palnis, Nellore District.
Alsocomus puniceus ..	Orissa Hills.
Anthracoceros malabaricus ..	Chota Nagpur.

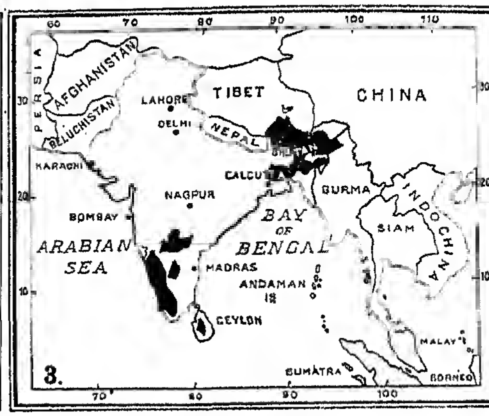
I would also like to make it clear that the species described as 'South-West' forms have been arbitrarily chosen as there is no hard and fast definition of this term. The matter has also been looked at entirely from the point of view of Indian ornithology with little or no reference to the neighbouring countries. To obtain a true



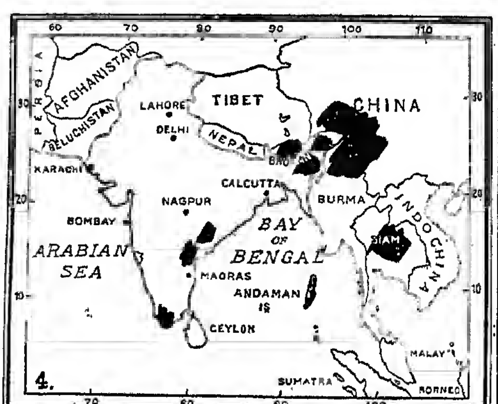
Oriolus chinensis



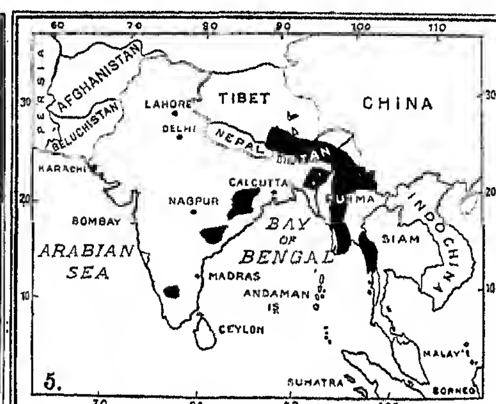
Geokichla wardi



Alseonax muttui



Phragmaticola aedon



Mixornis rubricapilla

idea of the general trend of distribution and migration it would be necessary to take into consideration allied forms in the neighbouring countries, i.e., not only in China and Malaya but also in Madasgacar and Africa. The flow of migration from China would have to be compared and co-ordinated with the Palaearctic elements which come in from the north-west and overlap much about the same area.

The data handled are by no means complete. All the information is haphazard and piecemeal covering widely scattered areas. The more one studies a problem of this kind, the more one realizes the insufficiency and superficial character of the work which has so far been done and how totally inadequate it is for formulating new theories. I must also confess that I have not had the opportunity of recently looking up the geological and other data of this area and have no idea as to how this fits in with the alternative Eastern Ghats route suggested above.

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SIMILARITY BETWEEN THE COLLARED SCOPS OWLS OF MALAYA AND PENINSULAR INDIA.

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Yet another example of the faunal similarity between Malaya and Peninsular India is provided by the Collared Scops Owl, *Otus bakkamoena* Pennant (Fam. Asionidae). In a recent examination of the various alleged subspecies of this owl, Roonwal and Nath (1949) have concluded that about six subspecies are recognizable in India, viz., *bakkamoena* Pennant, *plumipes* Hume, *deserticolor* Ticehurst, *lettia* Hodgson, *manipurensis* Roonwal and Nath and *gangeticus* Ticehurst (with *marathae* Ticehurst probably as a synonym). Malayan birds had been named *O.b. lempiji* Horsfield, 1821, but are really inseparable from *O.b. bakkamoena*. Roonwal and Nath (p. 165) write: 'We are quite unable to differentiate between *O.b. bakkamoena* for South India and *O.b. lempiji* from Malaya. This is evidently an example of the faunal similarity between the Malayan region and Peninsular India.'

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A NOTE ON THE DISTRIBUTION OF CHELONIANS OF PENINSULAR INDIA WITH MALAYAN AFFINITIES.

By K. C. JAYARAM, *B.Sc., Assistant, Zoological Survey of India, Indian Museum, Calcutta.*

(Communicated by Dr. S. L. Hora, F.N.I.)

In dealing with the zoogeography of Chelonia and other reptiles, Smith (1931, p. 16) was greatly struck by the discontinuous distribution of certain Malayan forms into the Peninsula of India and remarked:

> 'It seems equally certain that the Indo-Chinese hill tortoises, *Testudo elongata* and *Geoemyda tricarinata*, did not extend their range into the Peninsula of India (Chota Nagpur) by crossing the Gangetic Plain. True hill species for this reason are of greater interest and value in the study of zoological distribution than lowland forms. They are just as much isolated by the conditions under which they live as if they inhabited islands, and their occurrence upon widely separated mountain ranges is good evidence that a more direct connection between those ranges existed in past times than is to be found today.'

Hora (1948) has recently discussed the anomalous distribution of some of the Chelonians and shown that hill tortoises of Malayan affinities probably extended their range into the Peninsula of India by migrating along the Vindhya-Satpura mountains which were at one time continuous and higher, and were connected with the Eastern Himalayas and the Assam Hills in the east and the Western Ghats in the west. The Garo-Rajmahal Gap probably did not exist at that period (Hora, 1944).

Of the two species of hill tortoises referred to by Smith, *Testudo elongata* Blyth, is found from north-eastern India to Tonkin and the Malaya Peninsula as far south as Penang. It is stated to be rare in the northern part of its range and comparatively common in the southern part.

Smith (1931, p. 143) included Annandale's *T. parallelus* from Chota Nagpur in the synonymy of *T. elongata* Blyth and also indicated the close affinity of *T. travancorica* Boulenger to *T. elongata* Blyth. Taking the distribution of these three forms into consideration, Smith remarked:

> 'Annandale in describing his *T. parallelus* notes its resemblance to *elongata*, and comments upon the fact that a form showing such close affinities to purely Indo-Chinese species should occur also in the Indian Peninsula. That it ever crossed the Gangetic Plain as we know it today is, of course, highly improbable. A more likely explanation is to be sought in the antiquity of *Testudo*, *T. elongata*, *T. parallelus*, and *T. travancorica*, being the descendants of an ancestor that once ranged over India and Indo-China when the geographical conditions of the country were very different from what they are today. *T. travancorica* has become just sufficiently distinct to be separated off from *T. elongata*, *T. parallelus*, in my opinion, has not.'

T. elongata Blyth inhabits hilly districts chiefly at low altitudes and has a remarkable capacity for withstanding heat.

Geoemyda tricarinata Blyth has a distribution similar to that of *T. elongata* Blyth—Chota Nagpur and the hills of Assam but not extending further into the Indo-Chinese Peninsula. It is almost terrestrial in habits and is a hill species. The distribution of this species strongly suggests the continuity of the Assam and the Chota Nagpur hills and the absence of the Garo-Rajmahal Gap at a time when this species was more widely distributed.

Besides the two species referred to above, attention may also be invited to the distribution and polymorphism of two other species, namely, *Geoemyda trijuga*

(Schweigger) and *Lissemys punctata* (Bonnaterre). The former is chiefly aquatic in its habits and vegetarian in diet. The species is divisible into five forms, namely, *G.t. trijuga* (Bombay, Mysore and Madras); *G.t. edeniana* (Theobald) (Burma); *G.t. indopeninsularis* Annandale (Chota Nagpur and N. Bengal); *G.t. coronata* (Anderson) (Cochin and Travancore) and *G.t. thermalis* (Lesson) (Ceylon, Ramnad and Maldive Islands). A map showing the distribution of the above-mentioned races of *G. trijuga* was given by Smith (1931, p. 97) and reproduced by Hora (1948, p. 299). There can be no doubt that the species was once widely distributed in the Indo-Chinese and the Indian subregions and its present polymorphism is due to isolation resulting from physiographic changes during the Tertiaries and later periods. The distribution of the race *G.t. indopeninsularis* from Chota Nagpur and Jalpaiguri (Eastern Himalayas) is again strongly suggestive of the continuity of the hill ranges of the two areas.

Lissemys punctata (Bonnaterre) is a polytypic species inhabiting India and Burma. It lives in ponds and tanks, feeds upon both animal and vegetable matter and is of a quiet and timid disposition. It has three races, namely, *L.p. punctata* (The Ganges and the Indus and their tributaries); *L.p. granosa* (Schoepff) (Indian Peninsula south of the Ganges and Ceylon) and *L.p. scutata* (Peters) (the Irrawaddy and the Salween Rivers). The distribution of this species suggests its wide occurrence all over India and Burma during the period when there was an Indo-Brahm or the Siwalik River and its present polymorphism can be traced to the dismemberment of this ancient river system. (Hora 1948, pp. 303, 308.)

The ecology and distribution of the chelonians referred to above would seem to support Dr. Hora's hypothesis of the continuity of the Vindhyas and the Satpuras with the hills of Assam and the Eastern Himalayas.

I wish to express my sincere thanks to Dr. S. L. Hora for help and guidance in the preparation of this note.

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REMARKS ON THE DISTRIBUTION OF SNAKES OF PENINSULAR INDIA WITH MALAYAN AFFINITIES.

By SUNDER LAL HORA, *D.Sc., F.R.S.E., F.N.I., Director, and* K. C. JAYARAM, *B.Sc., Assistant, Zoological Survey of India, Indian Museum, Calcutta.*

Smith (1943, p. 26), in his *Fauna* volume on Snakes, has pointed out that in connection with zoogeography the affinities of the fauna of the Malay Region with Ceylon and Southern India deserve special mention. He has stated that 'Only one genus of snakes, namely *Cylindrophis*, has this distribution, being found in Malaysia, Indo-China, and Ceylon, but not in Peninsular India.' We have, however, a number of other species of snakes found in Peninsular India which possess distinct Malayan affinities. The distribution and habits of such forms are discussed below. All nomenclative and distribution data are taken from Smith's *Fauna* volume on Snakes.

Genus **Cylindrophis** Wagler.

The Pipe Snakes of the genus *Cylindrophis* belong to the family Anilidae, of which three genera are known, two in the Oriental Region and the third *Anilius* in Tropical South America. This discontinuous distribution of the family shows its antiquity and takes us back to the geological period when Australia, Southern Asia, South Africa and South America were believed to have formed one big continent, the Gondwana Land.

The seven species of *Cylindrophis* are known from the Indo-Chinese Region, the East Indies and Ceylon, only two are recorded from the Indian and Indo-Chinese Subregions. *C. rufus* Laurenti, with two races, is known from Indo-China, S. of lat. 17°N., the Malay Peninsula and Archipelago (*C. rufus rufus*), and Tenasserim and Burma as far north as Myitkyina (*C. rufus burmanicus*). The second species, *C. maculatus* Linn., is a common snake of Ceylon and is found in the plains and hills at low altitudes. They are burrowing snakes of placid habits.

Genus **Ahaetulla** Link.

The 'Bronze Backs' snakes of the cosmopolitan family Colubridae are known from the Oriental Region to Australia. The distribution of the 'Painted Bronze-Back', *Ahaetulla ahaetulla* Linn. is of special interst. Two races of this species are known of which one has already differentiated itself into two colour forms through geographical isolation. The typical colour form 'A' of the race *Ahaetulla a. ahaetulla* is found throughout the Indo-Chinese Subregion from Bengal and the Eastern Himalayas to Southern China. It is common in the hills and plains. A colour form 'B' of this race with the markings reduced is found in Southern India. The second race, *Ahaetulla a. andamanensis* is found in the Andaman islands which were once continuation of the Arakan Yomas.

Genus **Chrysopelea** Boie.

Chrysopelea is another Colubrid genus which is found in the Oriental Region and the East Indian Islands. Three species are known from the Indian and Indo-Chinese Subregions—*C. paradisi* Boie from the Malay Peninsula and *C. taprobanica* Smith from Ceylon; the third species *C. ornata* Shaw is more widely distributed but is polytypic in constitution. There are two colour forms of *C. ornata* Shaw which

can be restricted to definite geographical areas. One of these forms A, with vertebral spots, is found in Ceylon and the Western Ghats south of the Goa Gap, while the other B, without the vertebral spots, is found in the 'whole of the Indo-Chinese region, extending in the north-west to the triangle in Upper Burma and the Darjeeling district and to Patna and Buxa in Bihar and Orissa; in the north-east to Tong-King and Southern China (Hong-Kong); south to lat. 6°N'. It may be noted that *C. taprobanica* Smith, endemic in Ceylon, has been hitherto regarded as a colour variety of *C. ornata* Shaw and though specific differences have now been found between them, their common ancestry cannot be doubted. It is possible to assume that the polytypic *C. ornata* Shaw has already budded off a new species in Ceylon.

Genus **Dryocalamus** Günther.

The Colubrid snakes of this genus are good climbers, small in size, gentle in disposition and nocturnal in habits. Five species are known from India, Indo-China, the Malay Region and the Philippines. Of these, three are known to occur in the Indian and Indo-Chinese Subregion. The Bridal Snake, *D. nympha* Daudin is found in 'Ceylon and Southern India as far north as lat. 12° 30′ on the western side, and Orissa on the Eastern (Wall)'. The second species *D. davisoni* Blanford occurs in Siam, Tenasserim, Burma, Cambodia, Cochin-China and Southern Annam. The distribution of the third species, *D. gracilis* Gunther, is discontinuous and of zoogeographical importance. It is found in Ceylon and Peninsular India (Annamalais, Cuddapah Hills, Berhampore in Orissa) on the one hand and False Island, off the coast of Arakan on the other.

Genus **Atretium** Cope.

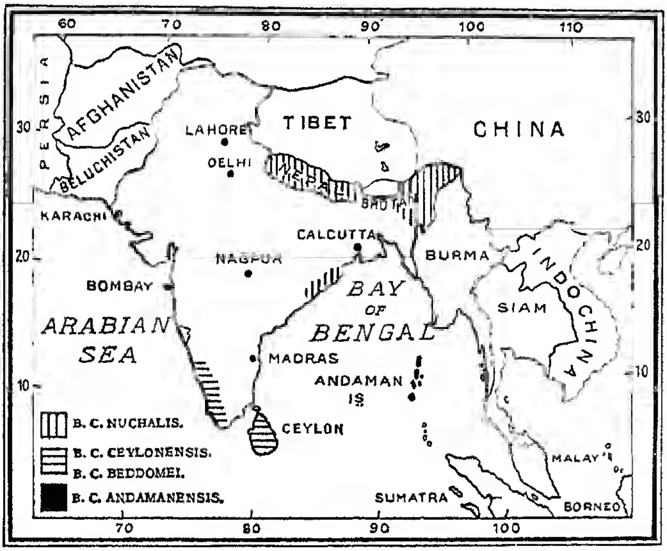
The genus *Atretium* of the family Colubridae is known from Ceylon, India and Yunnan. It is represented by two species. The Olivaceous Keelback Snake, *A. schistosum* Daudin is common in Ceylon and at Bangalore, but has also been recorded from the Annamalais, Wynaad, Mysore, U.P. and Orissa. The second species *A. yunnanensis* Anderson is known from Western Yunnan. In India proper, besides the hills of Peninsular India, the genus seems to be confined to the Satpura and Vindhya mountains or their spurs to the north or the south.

Genus **Rhabdops** Boulenger.

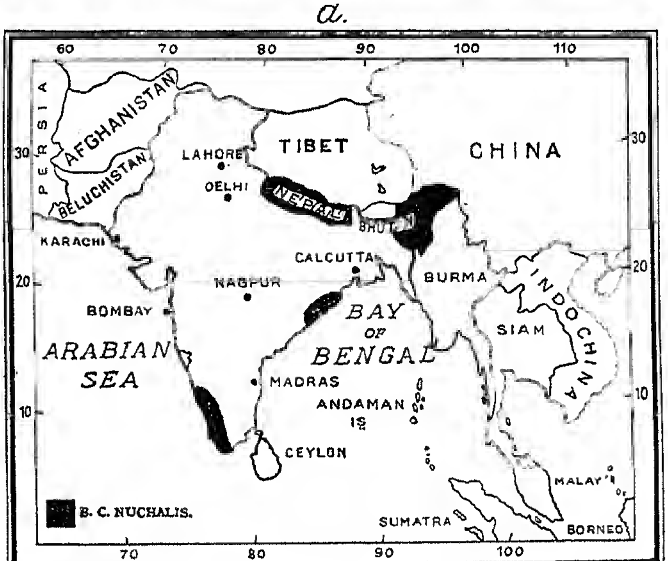
This Colubrid genus is found in Southern India, Burma and Yunnan and is known from two species. *R. olivaceus* Beddome is found in Wynaad (Western Ghats), while *R. bicolor* Blyth is known to occur in Assam (Khasi and Mishmi Hills), Burma (Kachin Hills) and Western Yunnan. These snakes are found in the hills and feed on worms and slugs.

Genus **Boiga** Fitzinger.

The Colubrid Cat Snakes of the genus *Boiga* are of great antiquity and are known to occur in Tropical Australia, Papuasia, Southern Asia and Tropical Africa. Some 25 species are known, of which 14 are found in the Indian and Indo-Chinese Subregions. The distribution of the polytypic Ceylon Cat Snake, *B. ceylonensis* Günther is of special interest from a zoogeographical point of view. This species is divided into four forms by Smith (p. 352) though other authors have recognized them as distinct species. The forms *ceylonensis* and *beddomei* are found in the Western Ghats and Ceylon; *nuchalis* is found in Western Ghats, Ganjam District, Nepal and Assam, and *andamanensis* is known from the Andaman Islands.



a.



b.

TEXT-FIG. *a*. Map of India and Farther East showing the distribution of the races of *Boiga ceylonensis*.

TEXT-FIG. *b*. Map of India and Farther East showing the distribution of *Boiga nuchalis*.

Genus **Dryophis** Dalman.

There are seven species of the Colubrid Whip Snakes (*Dryophis*) known from the Indian and Indo-Chinese Subregions. The genus is confined to the Oriental Région, Celebes and the Philippines. These snakes live on bushes and shrubs through which they can move with ease and great rapidity. One species, *D. nasutus* Lacépède the common Green Whip snake, has a discontinuous distribution over a wide range.

According to Smith (p. 377), its range is:—'Ceylon; Peninsular India, excluding the Ganges Valley West of Patna, B. & O. (*vide* Wall); Bengal; the Indo-Chinese region as far south as Rangoon in Burma; Siam; Cambodia; Cochin-China.'

Discussion.

The above-noted distributional records of the snakes *Cylindrophis rufus, Ahaetulla ahaetulla, Chrysopelea ornata, Boiga ceylonensis, Dryocalamus gracilis* and *Dryophis nasutus,* indicate one common feature—their absence from the areas between the Indo-Chinese Subregion in the East and Peninsular India and Ceylon in the West. From their ecology and habits, it is clear that they could not have crossed either the Bay of Bengal or the intervening dry tracts as they exist today. So the obvious explanation is that at some earlier period the climate of India was wetter in the regions of Chota Nagpur, Central Provinces and northern section of the Western Ghats so that climates similar to those now prevailing in the Assam Hills and the Eastern Himalayas in the east and the Malabar Tract of the Western Ghats in the west were uniformly spread over the intervening areas, thereby permitting the distribution of moisture and shade-loving animals from the east to the west. The hypothesis of the Satpura Vindhya Trend of mountains advanced by one of us in 1937 would appear to account for all the anomalies of distribution referred to above. The occurrence of some of these forms in Orissa, hills of the Eastern Ghats and U.P. shows that from the main migratory route of the Vindhya-Satpura trend the fauna was dispersed along the spurs to the north and south as a result of the epeirogenic movements consequent on the rise of the Himalayas. There is one other point to which attention may be invited. Some of the species, such as *Ahaetulla ahaetulla*, *Chrysopelea ornata* and *Boiga ceylonesis,* through segregation and isolation, have already become polytypic and in the case of *C. ornata* an entirely new species is now recognized in Ceylon. Other species are also exhibiting variations in colouration and even in morphological characters in the two widely separated regions. The distribution of the genera *Rhabdops* and *Atretium* is also of special interest or discussing the Malayan affinities of the fauna of Peninsular India.

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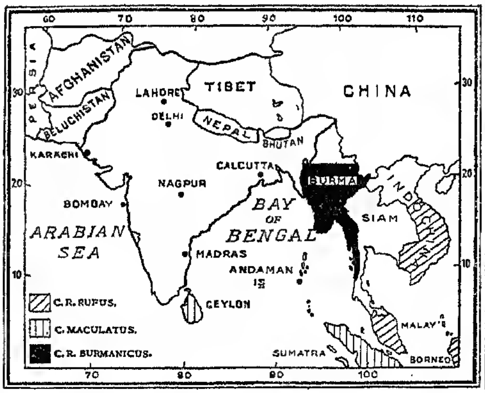

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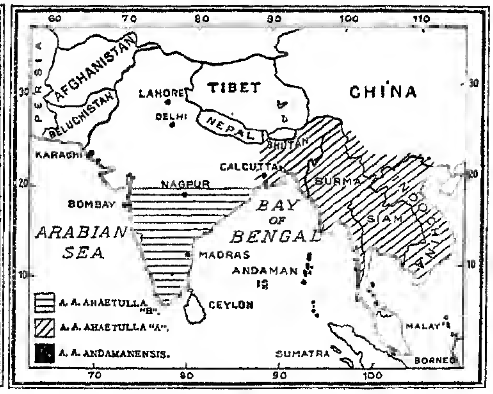

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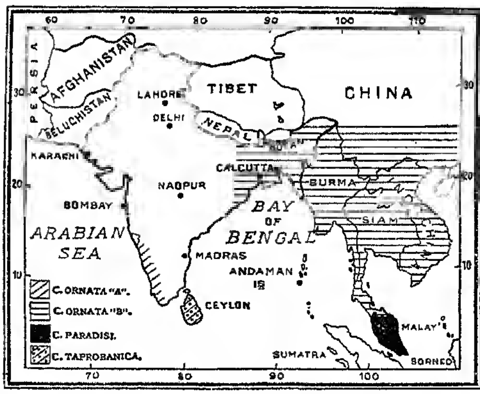

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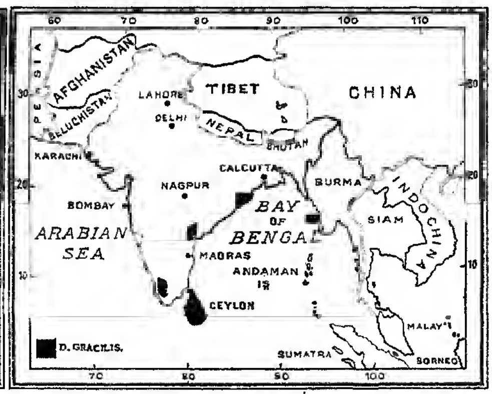

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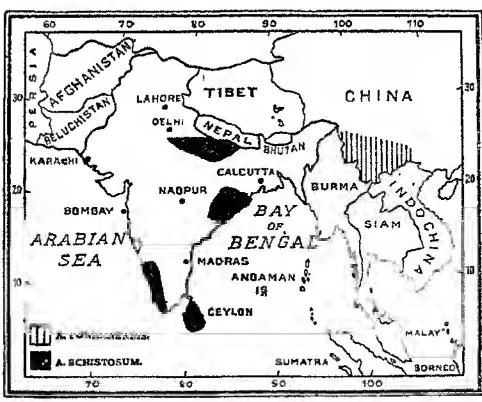

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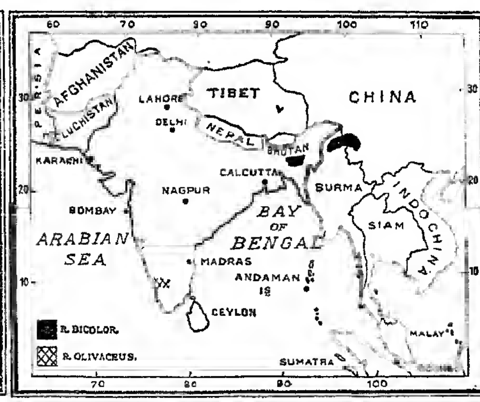

6.

FIG. 1.—Map of India and Farther East showing distribution of the genus *Cylindrophis* Wagler.
FIG. 2.—Map of India and Farther East showing the distribution of the colour forms and races of *Ahaetulla ahaetulla* Linn.
FIG. 3.—Map of India and Farther East showing distribution of the genus *Chrysopelea* Boie.
FIG. 4.—Map of India and Farther East showing distribution of *Dryocalamus gracilis* Günther.
FIG. 5.—Map of India and Farther East showing the distribution of the genus *Atretium* Cope.
FIG. 6.—Map of India and Farther East showing the distribution of the genus *Rhabdops* Boulenger.

DISTRIBUTION OF LIZARDS OF PENINSULAR INDIA WITH MALAYAN AFFINITIES.

By K. C. Jayaram, *B.Sc., Assistant, Zoological Survey of India, Indian Museum, Calcutta.*

(Communicated by Dr. S. L. Hora, F.N.I.)

In discussing the geographical distribution of lizards, Smith (1935, p. 15) remarked:

> 'The close affinities which certain Indo-Chinese and Malayan lizards have with others that inhabit Southern India—the northern part of the Indian Peninsula being without them—raises an interesting point in zoological distribution. The resemblance which *Dasia olivacea* bears to *D. subcaeruleum*, *Lygosoma maculatum* to *L. dussumieri*, and *Riopa bowringi* to *R. albopunctata*, is so close that one feels convinced that if one has not been derived from the other they must surely have had a common ancestor. The genus *Draco* has a similar distribution; *Varanus salvator* occurs in Ceylon and in Indo-China, but is absent from the whole of the Indian Peninsula; and there are similar parallels in distribution among the mammals, birds, fishes, and insects.'

These anomalies of distribution seemed very puzzling to Smith, as they had appeared to many other students of the fauna and flora of Peninsular India, and he put forward the following questions:—

> 'Why are they absent from Northern India? Have they died out in that area, or was there at one time a more southern route across the Indian Ocean by which they could travel?'

Hora (1948), has attempted to answer these questions on the basis of the Satpura Hypothesis and in the opening article of this series he has given many other details bearing on this hypothesis. In this article an attempt is being made to discuss the distribution and ecology of such lizards that are found in Peninsular India possessing distinct Malayan affinities. The data presented here are taken from Smith's *Fauna* volume on lizards. It will be seen from the following pages that many forms other than those referred to by Smith show Malayan affinity. I have, however, omitted *Varanus salvator* (Laurenti) from the list as it frequents sea-coast, particularly in the neighbourhood of estuaries, and thus the geographical barriers which restrict the distribution of other lizards are not effective in the case of this Common Water-Monitor.

Family Gekkonidae Boulenger.

Though Geckoes are found all over the hotter parts of the world, they are most numerous in the Australian and Oriental Regions. It is usual to regard Geckoes as an ancient group and their worldwide distribution also indicates considerable antiquity, no other family of the lizards, except the Scincidae being so widely distributed. It may, however, be noted that the House-Geckoes are frequently transported in cargoes of ships and the wide distribution of certain species is no doubt due to this cause. Though probably as ancient as the Jurassic Period, no fossil Geckoes have yet been found.

Genus **Cnemaspis** Strauch.

This is a widely distributed genus, being found in Africa, India, Indo-China and the East Indian Archipelago, and having a close ally in *Gonatodes* of America. Of the 20 species known, 13 are found in the Indian and Indo-Chinese subregions. Of these, 11 are restricted to the hilly regions of Southern India and Ceylon, the

remaining two are Indo-Chinese (*C. boulengeri*: (Strauch) Pulo Condor, off the coast of Cochin-China; *C. siamensis*: (Smith) Southern Tenasserim and Peninsular and South-Eastern Siam).

Smith (p. 73) has recorded *C. khandiana* (Kelaart) from 'Ceylon and hills of Southern India as far north as lat. 12°; Jog, North Kanara dist., ... the Andaman Islands; islands west of Sumatra', but remarked that 'perhaps introduced by man's agency into the Andaman Islands and the Malay Archipelago.'

Genus **Hemidactylus** Oken.

More than 60 species of the common House-Geckoes of the genus *Hemidactylus* are known from Southern Europe, Southern Asia, Africa, Tropical America and Polynesia. As many as 17 species are known from the Indian and Indo-Chinese subregions, and they exhibit various zoogeographical affinities. Two are, however, of special interest for this note and their distribution is discussed.

H. frenatus (Schlegel) is found in 'Southern India; Ceylon; Bengal; Indo-China; Hainan; Yunnan; Hong-Kong; southern China; the Malay Peninsula; the East Indian Archipelago and islands of the Indian Ocean; tropical Australian region; East Africa; St. Helena.' The wide and discontinuous distribution of the species shows its great antiquity.

H. bowringi (Gray) is known from India: Godavari Valley, Sikkim, Darjeeling and Chittagong; Burma; Myitkyina district, Thayetmyo, Minhla and Pegu; Yunnan-fu; Hong-Kong and S. China. The restricted distribution of this species in India and particularly its occurrence in Peninsular India in the Valley of the Godavari are of special interest.

Genus **Platyurus** Oken.

This genus has only two species. *P. platyurus* (Schneider) is found in Ceylon, Eastern Himalayas (Nepal, Sikkim and Darjeeling), Indo-China, Hong-Kong, Formosa and the East Indian Archipelago. The second species, *P. craspedotus*, inhabits the Malay Peninsula and Borneo. The genus as a whole is Indo-Chinese, but its occurrence in Ceylon is of great zoogeographical interest.

Genus **Gehyra** Gray.

This genus is of great antiquity as its distribution would suggest. According to Smith (p. 104), it is found in 'Mascarene Islands; Seychelles; the Oriental and Tropical Australian Regions; Polynesia; Mexico.' There are some 12 or 14 species, one of which only is found in the Indian and Indo-Chinese subregions. This species, *G. mutilata* (Wiegmann), is found in 'Ceylon; Southern Burma; Siam; French Indo-China; Hainan; the islands of the Indian Ocean; the East Indian Archipelago and Oceania.' Smith also found a specimen from Cochin relating to this species.

Genus **Hemiphyllodactylus** Bleeker.

Three species are known in this genus, of which two are found in the Indian and Indo-Chinese subregions. One of these, *H. typus* (Bleeker) is polytypic; *H.t. typus* is found in 'Ceylon; S. Burma (Pegu, Tavoy, hills between Burma and Siam); S.E. Siam (Klong Menao); Singapore; the East Indian Archipelago; islands of Oceania', and *H.t. aurantiacus* (Beddome) is being restricted to Southern India (Nilgiris, Shevaroy and Annamalai Hills). The second species, *H. yunnanensis* (Boulenger), is an Indo-Chinese form having so far been found in Yunnan, N. Laos and Upper Burma. The third species, *H. larutensis*, of the Malayan subregion which is closely allied to *H. yunnanensis*, is perhaps the northern representative of the Malayan form.

Genus **Lepidodactylus** Fitzinger.

The range of this genus extends from the islands of Oceania through the East Indies to Ceylon but the distribution is discontinuous. According to Smith (p. 116) *L. lugubris* (Dum and Bibr.) is 'widely distributed and apparently common in the islands of the S.W. Pacific Ocean; widely distributed but rarer, in the East Indian Archipelago and Malay Peninsula; Boulenger records it from Burma, the Andamans, and Nicobars, but I cannot trace the specimens to prove it. The only authentic records of its occurrence in the area included in this work are those by Deraniyagala from Ceylon, where it is evidently rare.'

Family Agamidae Gray.

The lizards of the family Agamidae are closely related to the New World lizards of the family Iguanidae. The former inhabit Asia, a few species extending their range into South-east Europe; Africa, excluding Madagascar; Australia and the New Guinea Archipelago, but not New Zealand. Agamids are, however, most numerous, both in genera and species, in the Oriental Region. Smith (p. 134) has recognized 19 genera from the Indian and the Indo-Chinese subregions and of these *Draco* and *Cophotis* deserve special mention from the zoogeographical point of view.

Genus **Draco** Linnaeus.

This genus of flying lizards is known from India, Indo-China and the East Indies. They are entirely arboreal in their habits, and feed on insects, grubs, etc. According to Smith, about 40 species of *Draco* are known, of which only 6 inhabit the Indian and Indo-Chinese subregions. One species is found in Southern India. Regarding the distribution of this genus, Smith observed:

> '*Draco*, therefore, affords a good example of discontinuous distribution. Between the South Indian species (*D. dussumieri*) and the Indo-Chinese forms, which do not range west of Assam, there is a gap of at least 1,000 miles in which no species has yet been obtained.'

The South Indian form, *D. dussumieri* (Dum. and Bibr.), is known from Madras, Travancore, Cochin, Malabar, Coorg, Karwar and Goa. It is often found in cocoanut and betel-nut plantations. The most westerly distributed species of the Indo-Chinese subregion is *D. norvilli* Alcock from the Naga Hills and Goalpara.

Genus **Cophotis** Peters.

This genus is known from two species, one inhabiting Ceylon and the other (*C. sumatrana* Hubrecht) * Sumatra and Java. *C. ceylonica* Peters is a slow-moving arboreal, viviparous in form and found about the moss-covered bases of tree-trunks in mountainous districts. It is found up to an altitude of 7,000 feet.

Family Scincidae Gray.

Though the lizards of this family are cosmopolitan in distribution, they are most numerous in the Australian Region and islands of the Western Pacific, the Oriental Region, and Africa. More than 600 species, distributed among some 40 genera, are known. Eighteen genera are found in the Indian and Indo-Chinese subregions. The vast majority are terrestrial in their habits but some have arboreal tendencies. A number of genera and species now found in the Indian Peninsula show distinct Malayan affinities and these are described:

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* Smith, M. A., *Bull. Raffles Mus.*, **3**, 26 (1930).

Genus **Mabuya** Rafinesque.

This is a widely distributed genus, of which more than 80 species are known; 15 being represented in the fauna of Indian and Indo-Chinese subregions. One species, *M. macularia* (Blyth), is polytypic and Smith (p. 264) has divided it into five forms as follows:—

Form 1.—India south of lat. 12°N., extending up the western side of the Peninsula as far north as lat. 16°. Also recorded from Ceylon.

Form 2.—The Deccan table-land or, roughly, the Peninsula north of lat. 12°, but not including the dry area of the North-West or the country east of and including Bihar and Orissa.

Form 3.—North-West India, Karachi to Dehra Dun.

Form 4.—Bihar and Orissa, Bengal and Assam.

Form 5.—This is more allied to Form 1 than to any other Form and is known from Burma, Siam, Cambodia, Southern Annam extending south to Kelantan.

The above distributional records leave no doubt that *M. macularia* (Blyth) must have had at one time a wide continuous distribution and that later through physiographic changes in the country became restricted to definite areas and as a result of isolation developed new geographic character. It is remarkable, however, that Forms 1 and 5 though separated by a very long distance are closely related.

Genus **Dasia** Gray.

This is a small genus of eight species, only three of which are known from the Indian and Indo-Chinese subregions. They are arboreal in habits. Of the three species, *D. olivacea* Gray is widely distributed, being found in Tenasserim, southern Siam and French Indo-China south of lat. 15°N.; Pulo Condore; the Andaman and Nicobar Is., the Malay Peninsula; the Natunas; Sumatra and the Mentawei Is.; Borneo and Java; *D. subcaerulea* (Boulenger) is closely allied to *D. olivacea* but is known only from Travancore. The third species, *D. haliana* (Haly and Nevil), is found in Ceylon. It is most likely that the Travancore and Ceylon forms are the descendants of the widely distributed *D. olivacea* (Gray).

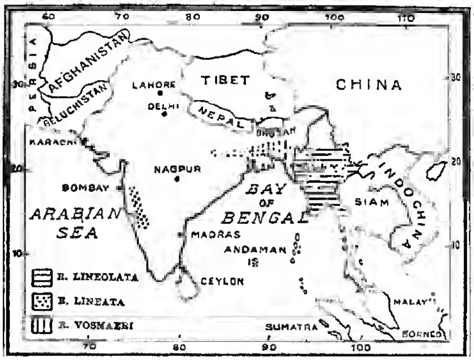
Genus **Lygosoma** Hardwicke and Gray.

The range of distribution of *Lygosoma* extends from Polynesia and Australia to Africa. Thirteen species of the genus are known from the Indian and the Indo-Chinese subregions. Of these, four are endemic in Ceylon, one is common to Ceylon and the Western Ghats between South Kanara and Trivandrum. One is found in North Assam. Three are found in the Eastern Himalayas but their range extends to other countries in the Far East. The remaining 4 species are found in Siam and other countries of the Far East. It will thus be seen that there is a gap of at least 1,000 miles between the forms occurring in Peninsular India and in the hills of Assam and the Eastern Himalayas. Smith (p. 15) has already drawn attention to the great resemblance between the Indo-Chinese *L. maculatum* (Blyth) and the South Indian *L. dussumieri* (Dum and Bibr) and to their common ancestry.

Genus **Riopa** Gray.

The range of this genus of Skinks extends from Polynesia and Australia to Southern Asia and Africa. These lizards are either terrestrial or subterrestrial. Of the 30 species known so far, 12 are found in the Oriental Region. Smith (p. 15) has already referred to the great resemblance between *R. bowringi* Günther of the Indo-Chinese subregion and *R. albopunctata* Gray of the Indian subregion, but it

may be of interest to discuss here the distribution of four other very closely allied species, namely, *R. lineolata* Stoliczka, *R. anguina* Theobald, *R. lineata* (Gray) and *R. vosmaeri* (Gray). It is likely that these are mere races of a single species. *R. lineolata* is known from Burma and is fairly widely distributed in the hilly districts; *R. anguina* is also known from Burma but its range is restricted to the Pegu District; *R. lineata*, with a more elongate body and of smaller size, though very much like *R. lineolata* and *R. anguina* is found in the Western Ghats between Poona and North Kanara and *R. vosmari*, resembling *R. lineata* very closely, is known from a single specimen collected in Bengal. The discontinuous distribution of these four closely allied species is of special zoogeographical significance.



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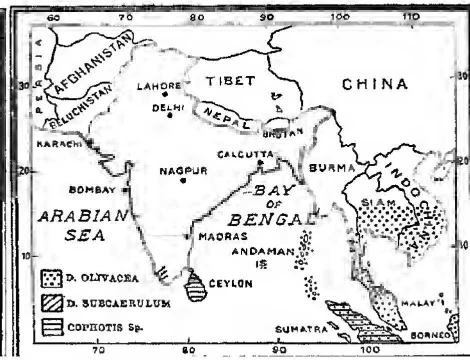

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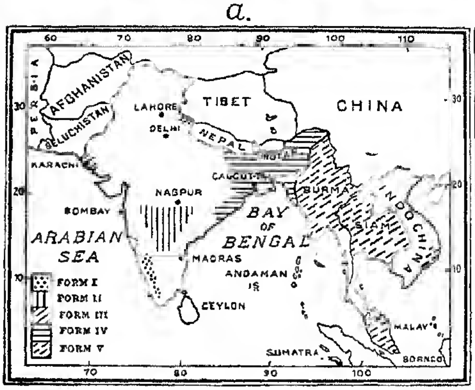

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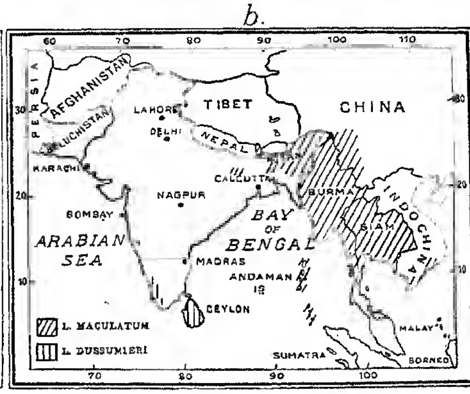

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TEXT-FIG. *a*. Map of India, Burma and Farther East showing the distribution of the genus *Riopa* Gray.

TEXT-FIG. *b*. Map of India, Burma and Farther East showing the distributiou of the genera *Dasia* Gray and *Cophotis* Peters.

TEXT-FIG. *c*. Map of India, Burma and Farther East showing the distribution of the various forms of *Mabuya macularia*.

TEXT-FIG. *d*. Map of India, Burma and Farther East showing the distribution of the genus *Lygosoma* Hardwicke and Gray.

Nine species belonging to the family Megascolecidae under this genus are mentioned in the *Fauna* volume. The distribution of the genus is the Palni and Nilgiri

Conclusion.

The anomalous distribution of the various genera and species referred to above can only be explained on the basis of continuity of range at one time. During the Tertiaries, at least, there was no direct land connection between the Malayan sub-region and Southern India as the Bay of Bengal is a very old feature of the physiography of India. Considering that most of the forms affected are characteristic of the hilly regions, and further considering the distribution of such forms as *Mabuya macularia*, it seems probable that the route of dispersal of the Malayan forms now locked up in Ceylon or the peninsula of India was provided by the Vindhya-Satpura trend of mountains which at one time stretched across India as a prominent ridge connecting the hills of Assam and the Eastern Himalayas on the one side and the Western Ghats on the other. It would also seem probable that the original centre of dispersal may have been Southern China whence they got distributed to the present-day extreme southern points through physiographic changes and have since died out in the intermediate regions.

Acknowledgements.

I am grateful to Dr. S. L. Hora for suggesting to me this problem for study, and for his constant guidance and assistance in the preparation of this note. I wish to record my thanks to Babu R. Bagchi, for help in the preparation of the distributional maps.

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Observations by Dr. M. A. Smith.

Dr. M. A. Smith of British Museum (Natural History) has very kindly made the following observations when the papers on Chelonians, Snakes and Lizards were sent to him for comments. The authors are grateful to him for this:—

The subject of discontinous distribution is always a fascinating one; unfortunately we can never be quite certain of the answer. I agree with most of what has been said in your papers but since I wrote my volumes of the Fauna I have changed my views on certain points.

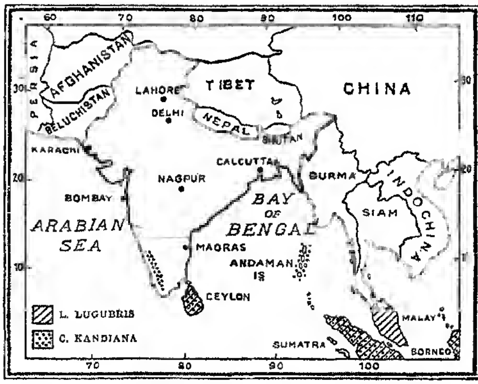
Where large genera are concerned such as *Lygosoma*, with huge numbers of species very closely related to one another I do not think that parallel evolution can be ruled out. When I was revising the genus *Lygosoma*—sensu Boulenger—I was surprised to find that a west African Skink—*Riopa guineense*—was indistinguishable from one that I had described from Siam *R. herberti*. There could be no question here of any geographical connection between the species; it was simply that the same set of characters had turned up twice. I think that this is what may have happened to *Lygosoma maculatum* and *L. dussumieri* and also to *Dasia olivaceum* and *D. subcaeruleum*.

Parallel evolution in the generic sense may account for the strange distribution of some of the geckos. *Gehyra, Platyurus* and *Hemiphyllodactylus* are clearly all derived from *Hemidactylus* and in the process of splitting off the same character may have turned up twice, so that the three first named genera are really polyphyletic assemblages and not natural genera which would account for their discontinuous distribution.

Atretium derived from *Natrix* may be another case and one could quote many more.

Draco and *Cylindrophis* cannot of course be covered by this argument. Either they came over the Satpura Vindhya range or they at one time inhabited all India and have since died out.

But the real struggle with our theories of distribution comes when we try to explain how *Trimeresurus, Microhyla* and the *Tapirs*, all found in the Malay region, got to South America.



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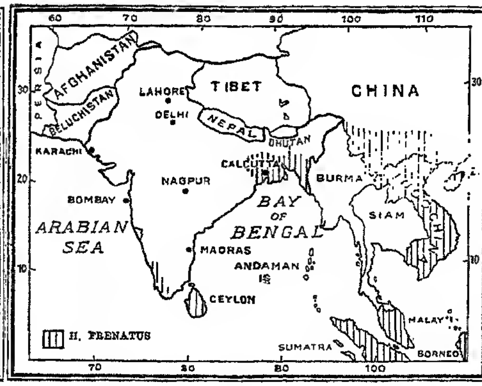

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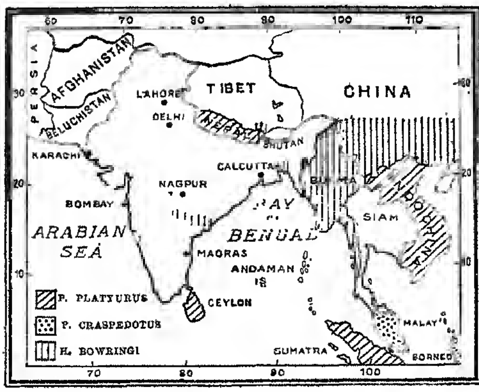

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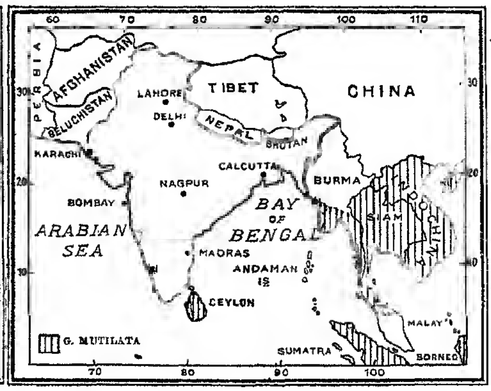

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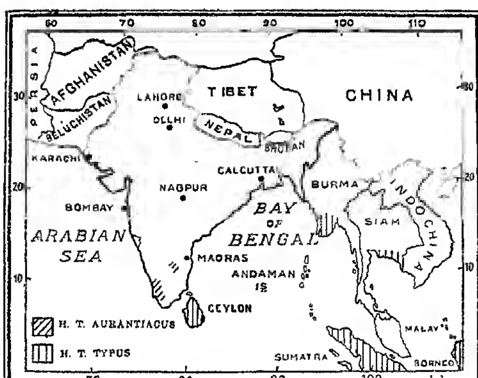

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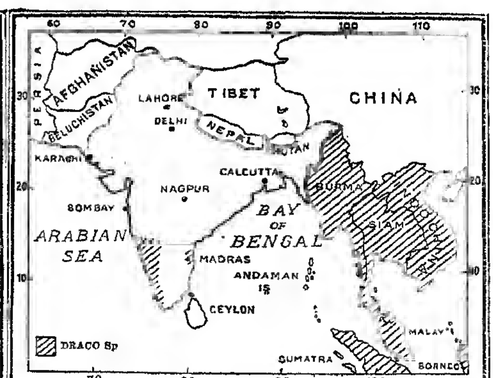

6.

FIG. 1.—Map of India had Farther East showing the distribution of the genera *Lepidodactylus* Fitzinger and *Cnemaspis* Strauch.

FIG. 2.—Map of India and Farther East showing the distribution of *Hemidactylus frenatus* Schlegal.

FIG. 3.—Map of India and Farther East showing the distribution of the genus *Platyurus* Oken and *Hemidactylus bowringi* (Gray).

FIG. 4.—Map of India and Farther East showing the distribution of *Gehyra mutilata* (Wiegmann).

FIG. 5.—Map of India and Farther East showing the distribution of the races of *Hemiphyllo-*

THE AGE OF THE BENGAL GAP.*

By Dr. A. K. Dey, *Geological Survey of India, Calcutta.*

(Communicated by Dr. S. L. Hora, F.N.I.)

1. The gap was certainly in existence in Lower Gondwana times. Direction of overlap, and existing dips, in the Rajmahal Hills indicate that no later renewal of the Satpura trend has had any appreciable effect on the altitude of the Gondwana rocks.

The Lower Gondwana gap served to connect the Bengal coalfields with the sub-Himalayan zone of Assam and Bengal Duars, and more or less aligns with the Krol Belt from south-east Nepal to the Simla area. It may have been superimposed on older trends in the period of Himalayan movements preceding the Upper Carboniferous (Altaid phase) or even earlier in the Palaeozoic.

2. It was certainly the estuary of a major river in the Lower Tertiary, as oyster-bearing clays replace the Sylhet limestone at and west of Tura. The marine development about the middle of the Miocene also extends right up to the gap from the eastward, and subsidence of the Bengal Delta region repeatedly occurred at least from Upper Cretaceous to the present day. The gap had therefore a continuous existence throughout the Tertiary and Quaternary periods and, as has been noted above, there is no evidence for any belt of uplift crossing it since earliest Gondwana times.

3. Going southwards, the Bengal gap and Godavari trough are about equidistant from the Lower Mahanadi trough. (All these contain Lower Gondwana deposits.) The Godavari trough at least shows evidence of repeated movements since Archaean times; that of the Lower Mahanadi approximates to, but does not coincide with, other ancient trends. Roughly in line with the Godavari trough is the west Vindhyan basin, compressed from the south-west by late renewals (in and after Vindhyan times) of movement in the Udaipur arm of the Aravallis. According to my colleague Mr. V. H. Boileau such complementary directions of movement are associated with major directions of crustal shortening in other countries and geological periods. (*Cf.* the depression across England from Cheshire to the south and south-east, crossing the Armorican trends of South Wales and south-west England on one side, and the Franco-Belgian coalfields, etc., on the other.) There is thus a distinct possibility that the Bengal gap was roughed out at a very early period as one of a series of such complementary warpings.

4. It is impossible, on available evidence, to accept the idea of a belt of hills across the Bengal gap, Chota Nagpur, etc., within the time-range of living animal species. The vast depression of temperature during the glaciation of the Himalayas (glaciers certainly come below 5,500 ft. and possibly well below 4,000 ft., in the Kangra Himalayas) seems to provide a more reasonable alternative. Mr. Boileau informs me that this idea has been accepted for a very long time as the explanation of 'islands' of 'Alpine' species on the higher mountains of Borneo—which are supposed to have been in continuity with the main habitat during the glacial periods. Moreover, if we remember correctly, Kingdon Ward has proved the return of floral species—previously driven out by glaciation—in the moister parts of the Tsangpo gorges of south-east Tibet, and in the Sikkim-Himalaya, though they have not been

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able to re-occupy drier areas in between. Their range must have been continuous when they were driven to lower ground in Assam, etc.

Mr. Boileau also informs me that Dr. Hora's hypothesis * (page 348) that 'so long as the relations between the distribution of land and sea were more or less the same as they are today, the present conditions can be presumed to have existed in the past also' is not a very sound argument. The shift of the temperate cyclone belt southwards from Europe into the Sahara during the Pleistocene glaciations is one of the best established facts of climatology, prehistory, etc.

A further point is that, during maxima of glaciation, so much water was tied up in polar and mountain ice-caps that the general sea-level was lowered considerably (50 fathoms around the entrance of the Persian Gulf, and about the same amount has been suggested from some Pacific islands) and the Bengal rivers cut down to levels well below their present courses (at least 400 ft. below sea-level in parts of West Bengal). This, with the vast run-off of glacial thaw-waters from the Himalayas, doubtless resulted in much more rapid currents in the lower reaches, and so 'torrential' fishes might have found them more suitable to their mode of living.

* 'Dating the period of migration of the so-called Malayan element in the Fauna of Peninsular India.'

DISCONTINUOUS DISTRIBUTION OF CERTAIN FISHES OF THE FAR EAST TO PENINSULAR INDIA.

By SUNDER LAL HORA, *D.Sc., F.R.S.E., F.Z.S., F.R.A.S.B., F.N.I., Director, Zoological Survey of India, Indian Museum, Calcutta.*

While commenting on the distribution of Himalayan fishes, with special reference to certain palaeogeographical problems, an attempt was made (Hora, 1937, pp. 251–259) to account for the occurrence of quite a large number of Eastern Himalayan forms in the hills of Peninsular India. It was then stated:

> 'As the Himalayas rose to a great height in the region of this isthmus (mostly the western part of the Assam Himalayas and eastern part of the Nepal Himalayas) all the evidence concerning the north-eastward extension of the Indobrahm seems to have been obliterated. The uplift movement was probably most active in this region as we find practically all the highest peaks of the Himalayas clustered round this area. This differential movement which probably occurred late in the Miocene period, must have obliterated all traces of the eastward extension of the Indobrahm and also acted as a barrier between the eastern and the western Himalayan fishes. *The new stocks of specialized hill-stream fishes from the east, not finding means to cross this barrier, were deflected towards south-west along the Satpura Trend which probably at that period stretched across India as a pronounced range from Gujarat to Assam Himalayas. From Gujarat the hill-stream fauna migrated towards the south along the Western Ghats and spread to the hills of the Peninsula in the extreme south.*' (Italics are now inserted.)

The hypothesis enunciated in the passage italicized in the above quotation was subjected to intensive field investigations with very interesting results. A summary of these investigations was given by me in 1944 (pp. 430, 431) and it was concluded that 'The results of the zoological survey of the various sections of the Satpura trend clearly indicate that at some remote period the fauna of this chain of hills had some means of continuity with that of the hills of Assam'. In the present-day topography of India, the Garo-Rajmahal Gap seemed to be the biggest hurdle in the acceptance of this hypothesis but an analysis of the geological evidence (Hora, 1944, pp. 431, 432) showed that even in post-Pliocene times block-faulting occurred in the Peninsula and the Garo-Rajmahal gap may be the result of these later block-faulting.

An investigation of the fish-fauna of the Rihand River (Hora, 1949, pp. 1–7) had lent great support to the Satpura Hypothesis, for species of fish hitherto known from the Western Ghats, such as *Glyptothorax annandalei* Hora, on the one hand and from the Eastern Himalayas, *G. horai* Shaw and Shebbeare, on the other, have now been found in the Vindhyas. Similarly the study of the palaeoclimates and palaeogeography have revealed that the Vindhyas and the Satpuras may have been much higher than what they are at present.

I propose to give below a few instances of discontinuous distribution, which strongly suggest the invasion of the so-called Malayan fauna to the Indian Peninsula, their subsequent isolation and consequent differentiation into genera, species or subspecies according to the degree of isolation and change in the environment. I wish to emphasize that hill-stream fauna is so specialized that its dispersal could only have been accomplished through the temporary or permanent connections of such streams. The idea of fortuitous dispersal of such forms must be abandoned once for all.

Family CYPRINIDAE.

Subfamily *SCHIZOTHORACINAE*.

Genus **Lepidopygopsis** Raj.

In 1941, Raj described a remarkable genus of Schizothoracine fishes from the Periyar Lake in Travancore and explained its distribution so far away from other

members of this Central Asiatic subfamily on the theory of 'Refrigeration of Climates' during the Pleistocene Glacial Age (Medlicott and Blanford, 1893, pp. 13–16). I have shown elsewhere (1949*a*, pp. 193–204) that the Himalayan Glaciation had no effect on the distribution of the freshwater and terrestrial animals of Peninsular India and pointed out the probability of the Vindhya-Satpura trend of mountains and the Western Ghats having served as the routes of migration of the hill species. The Schizothoracinae are Cyprinoid fishes, mostly confined to the highlands of Central Asia, with several forms occurring in Yunnan in the east and Waziristan-Seistan in the west. They are also abundant in the valley of Kashmir. Two genera, *Schizothorax* and *Oreinus*, are found on the southern face of the Himalayas, the latter being adapted for life in swift currents. The Travancore genus, *Lepidopygopsis* Raj, would seem to have been derived from a *Schizothorax*-like ancestor of the Eastern Himalayan region which migrated in ages past over the Satpura trend of mountains and down the Western Ghats to Travancore and there, through subsequent topographical changes, became isolated and differentiated from the parent stock. In any case, it is a remarkable case of discontinuous distribution.

Subfamily *Cyprininae*.

Genus **Mystacoleucus** Günther.

The most outstanding character of this Cyprinid genus is the presence of a procumbent predorsal spine. Weber and de Beaufort gave its distribution as 'Sumatra, Java, Borneo and Malacca'. In 1937, I discussed the systematic position, geographical distribution and evolution of the Cyprinoid genera with a procumbent predorsal spine and pointed out that *Rohtee ogilbii* Sykes also belonged to that group and definitely referred it to the genus *Mystacoleucus*. Smith (1945, p. 129) commented on this assignment. Without going into nomenclative discussions at this place and taking the Cyprinidae group with such a characteristic spine as a whole, it is very significant to note that such fishes are found in China (Formosa, Hainan, Fukien and Szechwan), Siam, Lower Burma, Malay Peninsula, Sumatra, Java and Borneo on the one hand and in Deccan on the other. Such a wide gap in the distribution of the Mystacoleucus group of fishes is of great Zoogeographical interest. The group has already become differentiated into several genera and it seems likely that the Deccan form with a much longer anal fin may have to be considered distinct from all other genera.

Genus **Thynnichthys** Bleeker.

Besides the Homalopteridae, this is the only Malay fish which was recorded from Peninsular India by earlier ichthyologists. Weber and de Beaufort (1916, pp. 121–132) have recorded three species from Sumatra and Borneo, but since then the range of *T. thynnoides* has been found to be fairly extensive. Smith (1945, p. 209) has given an account of its known distribution and stated that it had so far been recorded from Indo-China, Siam, Malay States, Sumatra and Borneo. In Peninsular India, there is only one species, *Thynnichthys sandkhol* (Sykes), which is found in the Godavari and Kistna river systems. I have not yet studied the systematics of the members of this genus but there can hardly be any doubt that the Malayan and the South Indian species are evolved from a common ancestral stock.

Genus **Osteochilus** Günther.

In 1942 (Hora, 1942, p. 5) it was pointed out that Day had referred a certain form from Malabar to the genus *Osteochilus* and had even proposed a name for it (*O. malabaricus*), but he had never described it. Day's three species of *Scaphiodon* from the Western Ghats did not belong to that genus but were allied to *Osteochilus*.

After discussing their systematic position, I grouped them into two subgenera of *Osteochilus* and generally discussed the evolution and distribution of the genus. It then became clear to me that the genus *Osteochilus* is polytypic and that its species from Southern China, Indo-China, Siam, Malay Peninsula, the Indo-Australian Archipelago and Burma, are greatly in need of revision and regrouping. The genus, as recognized at present, is found in the countries of South-Eastern Asia as far west as Burma and then three of its representatives appear in the Western Ghats. The discontinuity in the distribution of the genus and the differentiation of its South Indian representatives into subgenera is of considerable interest.

Genus **Schismatorhynchus** Bleeker.

In giving the distribution of this remarkable Cyprinid genus, Weber and de Beaufort (1916, p. 217) have remarked:

> 'Fresh water of Indo-Australian Archipelago (Sumatra and Borneo); perhaps also represented on the Indian continent.'

Presumably the authors had in mind *Labeo nukta* (Sykes) from the Deccan, being the only species of *Labeo* found in India in which a proboscis is present on the snout. In 1942, I (pp. 10–13) discussed the systematic position of this species and definitely referred it to *Schismatorhynchus*. The differences in the structure of the lips and associated parts in the Indo-Australian and Indian species were so remarkable that a separate subgenus *Nukta* was proposed for the Deccan form. Here again, the points worth noting are:—

(i) General similarity between *Sch. heterorhynchus* (Blkr.) from Sumatra and Borneo and *Sch. nukta* (Sykes) from the Deccan.
(ii) Discontinuity in the distribution of the genus leading to isolation of the two known forms.
(iii) Differentiation resulting from isolation leading to differences in structure of a subgeneric rank.

Family *Homalopteridae*.

The family Homalopteridae comprises small loach-like fishes found in torrential streams of southern and eastern Asia. In 1932, the family was monographed by me and, besides classification, the bionomics and evolution of its various members were discussed. It was then pointed out that the family is polyphyletic and is readily divisible into two subfamilies on the structure of its paired fins. In addition to the osteological characters, the most obvious difference is in the degree of simplification of the rays of the paired fins. In the Homalopterinae, which appear to have been derived from the Cyprinidae, at least 2, and in some genera 3, 4 or 5, of the anterior pelvic rays are simple, and in the various genera from 4 to 13 of the anterior pectoral rays are simple. In the Gastromyzoninae, which appear to be derived from the Cobitidae, only one ray in the pelvic and pectoral fins is simple.

Since the publication of my monograph, there has been considerable further expansion of our knowledge of these fishes and several new genera and species have been described. This is not the place to review the systematics of the newly described forms, but from a zoogeographical point of view the old distributional facts have become still further emphasized. The isolation of the Homalopterinae in the southern part of the Western Ghats and its differentiation in that far flung corner of the range of its distribution into two remarkable genera, *Bhavania* Hora * and

* For a revision of the Homalopterid fishes of Peninsular India, Hora (1941, pp. 221–232) may be consulted.

Travancoria Hora, are facts of great zoogeographical importance. The discovery of *Balitora brucei* in Peninsular India though racially distinct from the typical form occurring in the Eastern Himalayas and Assam, indicates the source from which the South Indian forms have been derived. The Homalopterinae are found in Southern China, Eastern Himalayas, Assam and Chittagong Hills, Burma, Siam, Malay Peninsula, Sumatra, Java and North-Central Borneao in a more or less continuous range and in Peninsular India. The isolation of the Homalopterinae in the Island of Hainan in the East and in the extreme south-west of the Indian Peninsula is a remarkable fact of distribution.

Family *Siluridae*.

Genus **Silurus** Linnaeus.

In 1936, I recognized two Indian species in the genus *Silurus* on the number of mandibular barbels—*S. wynaadensis* C. & V. with four barbels, from Wynaad in the Western Ghats and *S. cochinchinensis* from the Eastern Himalayas, Assam and Burma. Bhimachar and Rau (1941, pp. 141–152) in recording the species *cochinchinensis* from Mysore have shown that the larger number of barbels is a juvenile character and, therefore, *wynaadensis* cannot be recognized as a species distinct from *cochinchinensis*. Smith (1945, p. 333) recorded it from Peninsular Siam. The species is known from Hainan, Cochinchina, Siam, Burma, Assam, Eastern Himalayas and the Western Ghats. The occurrence of the same species over such a wide area and its discontinuous distribution are points of considerable interest.

Family *Bagridae*.

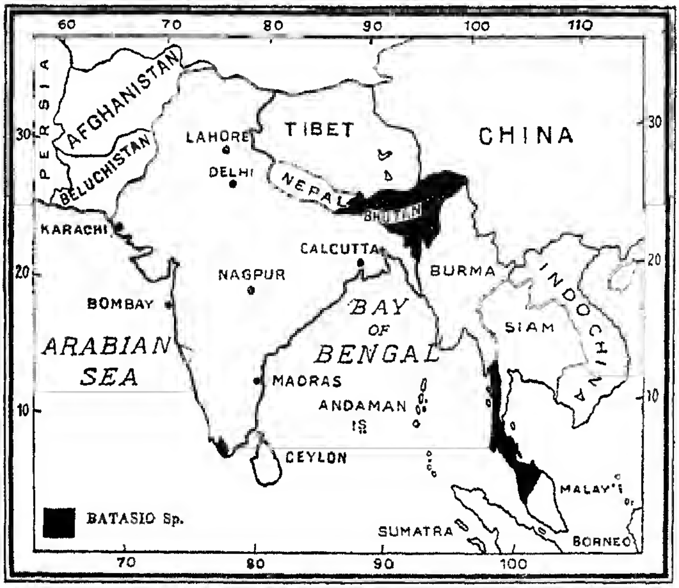
Genus **Batasio** Blyth.

This is a genus of Bagrid catfishes of small size which inhabit hill streams at the bases of hills. Only three species are known (Hora and Law, 1941, pp. 28–42, pl. ii). *B. batasio* (Hamilton) is found only in the foothills of the Eastern Himalayas; *B. tengana* (Hamilton) has so far been recorded from the Eastern Himalayas, Assam, Tenasserim, Mergui and Perak, possibly a race of this species *havmolleri* Smith is found in Peninsular Siam (Ronpibun) and the third species *B. travancoria* Hora is known only from Travancore. The occurrence of the genus in Travancore at such a great distance from the Assam Hills lends considerable support to the Satpura Hypothesis.

Family *Sisoridae*.

Genus **Gagata** Bleeker.

This is a genus of Sisorid catfishes which are found at the bases of hills or are sometimes washed down into rivers in their neighbourhood. The Indian species of the genus were revised by Hora and Law (1941, pp. 9–27) who recognized only five species from India and Burma. *G. gagata* (Ham.) is known from the Ganges, Brahmaputra and Irrawadi river systems; *G. cenia* (Ham.) from the Himalayas, Orissa, Assam, Burma and Siam (Salween River); *G. viridescens* (Ham.) from Bengal and Assam; *G. nangra* (Day) from the Himalayas and *G. itchkeea* from the Western Ghats (Deolali, Poona, Satara and Coorg). There is only one extra-Indian species, *G. schmidti* Volz from Sumatra (Simbolan hills). The occurrence of the genus in the Western Ghats and Sumatra at so far a distance from the main centre of distribution is of special zoogeographical significance.



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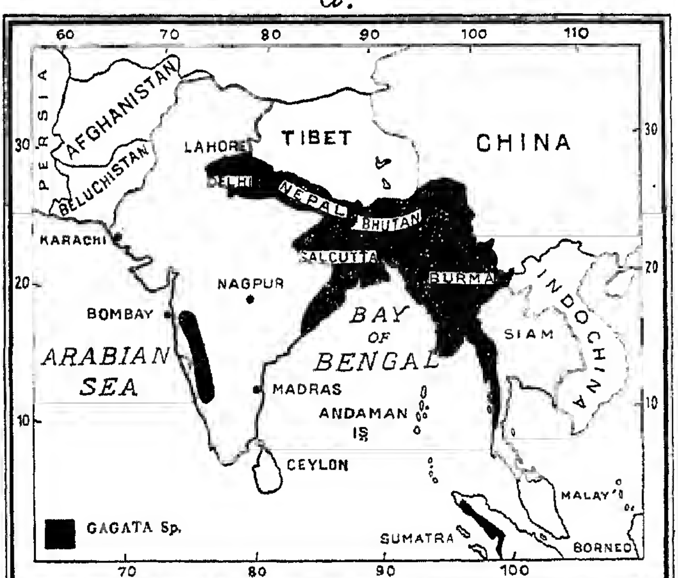

b.

TEXT-FIG. *a.* Map of India and Farther East showing the distribution of the genus *Batasio* Blyth.

TEXT-FIG. *b.* Map of India and Farther East showing the distribution of the genus *Gagata* Bleeker.

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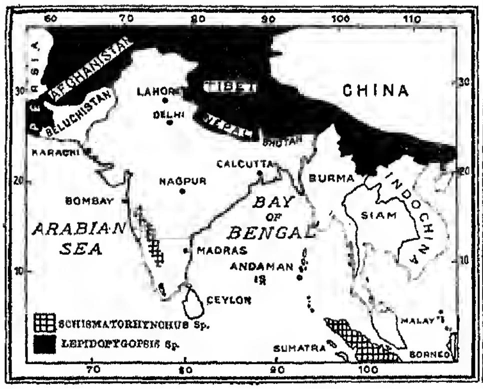

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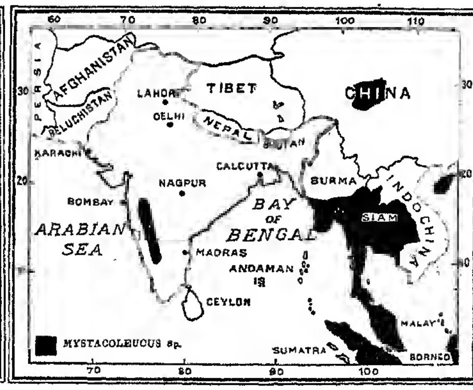

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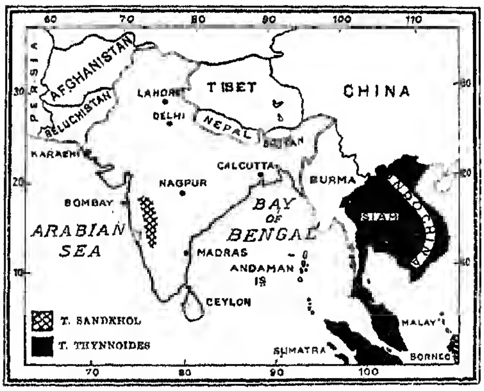

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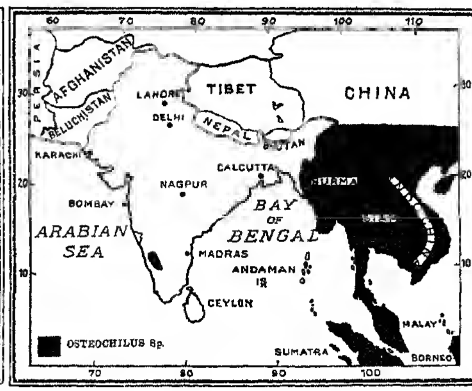

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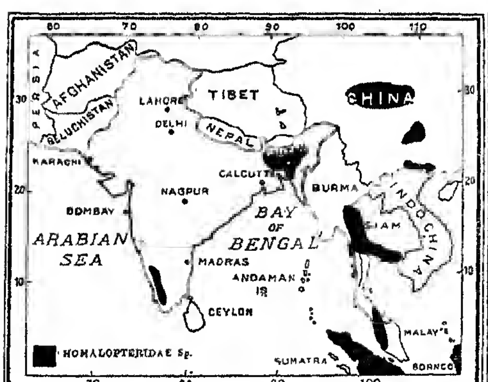

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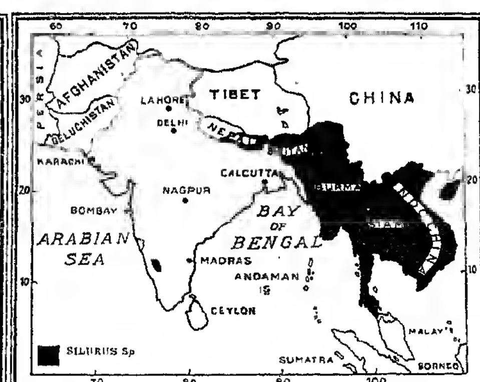

6.

FIG. 1.—Map of India and Farther East showing the distribution of the genera *Schismatorhynchus* Bleeker and *Lepidopygopsis* Raj.
FIG. 2.—Map of India and Farther East showing the distribution of the genus *Mystacoleucus* Günther.
FIG. 3.—Map of India and Farther East showing the distribution of the genus *Thynnichthys* Bleeker.
FIG. 4.—Map of India and Farther East showing the distribution of the genus *Osteochilus* Günther.
FIG. 5.—Map of India and Farther East showing the distribution of the family Homalopteridae.

REMARKS ON THE DISTRIBUTION OF ANNELIDS (EARTHWORMS AND LEECHES) OF PENINSULAR INDIA WITH MALAYAN AFFINITIES.

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(Communicated by Dr. S. L. Hora, F.N.I.)

Introduction.

As early as 1916, Stephenson (p. cxvii), in a paper read at the Indian Science Congress, remarked:

> 'It is not necessary to suppose with Michaelson, that the land connection must have extended across the Bay of Bengal; recent discoveries in the Abor Country renders it possible to suppose that the Oligochaete immigrants took a path round the head of the Bay.'

Again in his volume in the *Fauna* series on Oligochaeta (1923, p. 27), he stated:

> 'The meaning to be attached to these facts of distribution is not in all cases clear; it may mean that these genera evolved outside India, entered round the head of the Bay of Bengal and have left colonies behind them in the passage over this region.'

In this article an attempt is being made to elucidate the distribution of the Annelids of Peninsular India with Malayan affinities. The names of genera, species and races, and ecological data concerning them, range of distribution, etc., are taken from Stephenson's *Fauna* volume on Oligochaeta.

OLIGOCHAETA.

Genus **Drawida** Michaelsen.

This genus of large Indian Earthworms belongs to the family Moniligastridae, which is mostly found in S. India and Ceylon, though its range extends to Burma, Bengal and the E. Himalayas, etc. One species is even known from Borneo. Two species of Peninsular India are of special zoogeographical interest. *D. jalpaigurensis* is found at Jalpaiguri at the base of the Eastern Himalayas. Its atrium resembles that of *D. travancorensis*, which is found in Kottayam, Travancore, S. India. The occurrence of these two hill species, closely resembling each other, found on either side of the present-day Garo-Rajmahal Gap which is separated by a distance of over a thousand miles lends support to Dr. Hora's Satpura Hypothesis. Another species, *D. pellucida*, having four varieties or forms restricted to different regions, is also significant. Their distribution is as follows:—*D. pellucida* (forma typica)—Ootacamund, and Naduvattam, S. India; Upper Rotung, Abor Country; *D. p.* var. *bournei*—Ceylon, Vakvalla, Bentola, Kaniya (amongst roots in damp ground near the outflow of a hot spring), Kandy, Colombo Museum Gardens and Trincomali; *D. p.* var. *stewarti*—Rotung and Renging, Abor Country; E. Himalayas and *D. p.* var. *pallida*—Shencottah, E. side of W. Ghats, Travancore. The discontinuous distribution of the species as a whole and particularly of the race *D. pellucida* (forma typica) shows great affinities with the forms found in the Assam Hills and the E. Himalayas on the one hand and the hills of the Indian Peninsula and Ceylon on the other.

Genus **Plutellus** E. Perr.

Nine species belonging to the family Megascolecidae under this genus are mentioned in the *Fauna* volume. The distribution of the genus is the Palni and Nilgiri

Hills, and Cochin, S. India, Ceylon; Darjeeling Dist., and Abor Country, E. Himalayas and outside India, Australia, Tasmania and N. America.

Genus **Perionyx** E. Perr.

This Megascolecid genus has both peregrine and ordinary species. Excluding the former, the genus is restricted to the Western Himalayas (neighbourhood of Simla and Kumaon Hills), Eastern Himalayas, Abor Country, Assam, Burma, Bengal, Bombay and neighbourhood (as far as Belgaum to the South), South India (Mysore, Nilgiris) and Ceylon. Stephenson spotted the distribution of this genus on a chart (p. 167, Chart III) and has remarked:

> 'If the Indian localities are indicated on a map, the distribution is seen to be a double one; the main home of the genus is in the E. Himalayas, stretching W. to Simla and E. into Burma; but it has also established itself in a line along the S.W. of peninsula from Bombay to Ceylon. These are regions of greatest rainfall. I have mentioned as peculiarities of the genus that it has not infrequently been found in wood or on trees under the leaves of trees, or even in running water.' (p. 320.)

HIRUDINEA.

In his *Fauna* volume on Leeches, Percy Moore (1921, p. 113) has remarked on the anomalous distribution of certain forms and has stated:

> 'The remainder of India, including Ceylon and Burma, belongs definitely to the Indo-Malayan Region with some African affinities. Ceylon and southern portion of the peninsula approach the Malayan and Philippine Archipelagos rather more closely, and the northern Himalayan region, in addition to the peculiarly rich fauna of true land-leeches, as will be pointed out in greater detail under the genus *Haemadipsa*, shows some Chinese intrusions.'

I shall discuss here the distribution of only those species of Peninsular India which show Malayan affinity.

Genus **Herpobdelloidea** Kaburaki.

Herpobdelloidea lateroculata is a small leech, remarkably planarian-like in life. It is found in small streams and ponds moving rapidly along the surface of water-plants. The species was described by Kaburaki from Bushampur and Saugor (Central Provinces); other records are 'outside Farm caves in Moulmein, Lower Burma'; 'Khardi Nadi, Loktak Lake, Manipur, Assam, 2,600 ft.'; 'Coviloar'. The discontinuous distribution of the species strongly supports the Satpura Hypothesis of Dr. Hora.

Genus **Myxobdella** Oka.

This genus belongs to the family Hirudidae and comprises two species. One of these, *M. annandalei* is found in India as well as in China. It inhabits hill streams at slight elevations and is found clinging under stones. The range of its distribution is: Hongkong, Yercaud, Madras, Dawna Hills and Lower Burma.

Genus **Haemadipsa** Tennet.

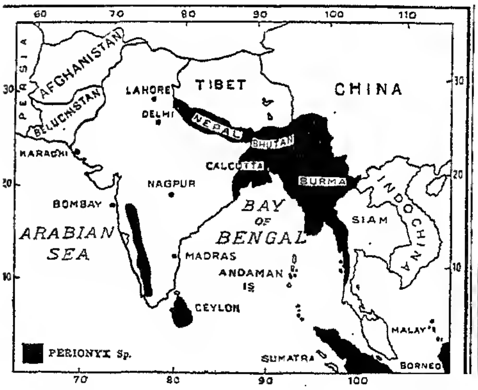
This is a polytypic genus having several colour varieties associated with land planarians having a nearly identical colour pattern, a resemblance that might be described as mimetic. *H. zeylanica* is an interesting polytypic species with 4 sub-species. The *forma typica* ranges widely, but discontinuously, from sea-level in Ceylon to above 12,000 feet in the Himalayas. These leeches are of large size and very vicious in their habits. The distribution of the *forma typica* and its subspecies are given below:—

H. zeylanica (*forma typica*):—Japan, Philippines, Malay Archipelago and neighbouring Island groups and Ceylon. *H.z. cochiniana*:—Kavalai, Cochin State; Nilgiri Hills; Madras; N. Kanara, Bombay. Taken from near sea-level to 3,500 feet. It is a good climber owing to its highly developed prehensile papilla.

H.z. agilis:—Naini Tal, Almora, Kumaon Lakes, Western and Eastern Himalayas at 5,500 feet altitude.

H.z. montivindicis:—Darjeeling district, Sikkim, Assam. Abundant in damp ravines and dripping forests of high levels from 1,800 to 9,500 ft. altitudes.

Another mountain species of the same genus is also of interest. *H. montana* occurs widely at separated points, namely, 'Kukkal, in the Palni Hills, Madras State at 5,500–6,500 feet elevation; near Darjeeling at 7,000–8,000 ft., Dawna-hills (eastern side), Burma.



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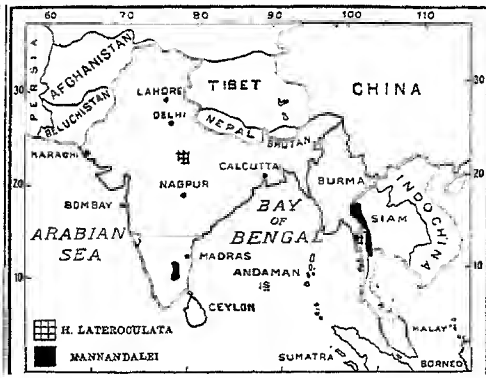

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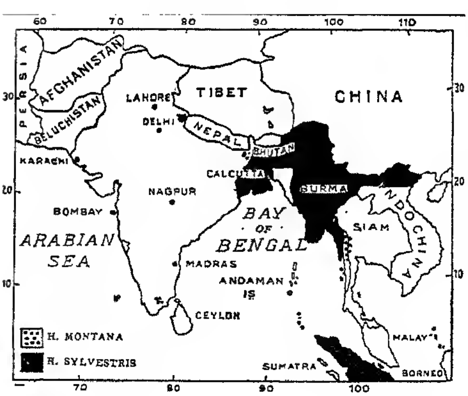

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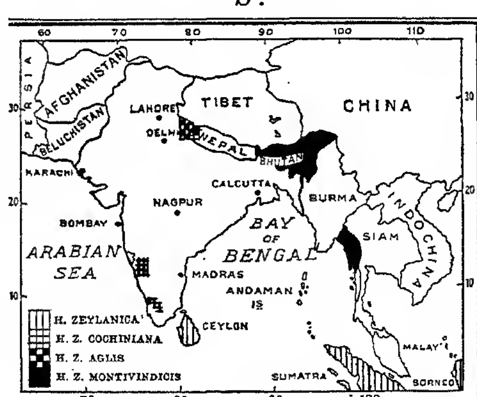

d.

TEXT-FIG. *a*. Map of India and Farther East showing the distribution of the genus *Perionyx* E. Perr.

TEXT-FIG. *b*. Map of India and Farther East showing the distribution of the genera *Myxobdella* Oka and *Herpobdelloidea* Kaburaki.

TEXT-FIG. *c*. Map of India and Farther East showing the distribution of *Haemadipsa* Tennet.

TEXT-FIG. *d*. Map of India and Farther East showing the distribution of *Haemadipsa zeylanica* and its races.

The third and the last species belonging to the same genus is *H. sylvestris*. This is mainly a terrestrial form, being found at 3,000 ft. elevation. The distribution is Kerenni Mts. of Lower Burma, Java, Sumatra, Tonkin, Burma, Darjeeling district, Bengal (Calcutta and environs), Naini Tal (W. Himalayas). It shows clearly that 'the stronghold of this species is in the hills of Assam, especially in the neighbourhood of Shillong and Cherrapunji and in Cachar'. The occurrence of this species on either side of the Garo-Rajmahal Gap is noteworthy.

Conclusion.

The above-noted distributional records of Earthworms and Leeches bring out one common feature—their absence in the plains of Northern India. Some species occur on either side of the Garo-Rajmahal Gap, and are locked up in various stations along their migratory route. As a result of long isolation some have already budded out new subspecies in their new habitats. The distribution of the species and subspecies lends support to the Vindhya-Satpura Hypothesis of Dr. Hora, which enables us to explain these anomalies of distribution.

Acknowledgments.

I wish to express my sincere thanks to Dr. S. L. Hora, for his supervision and guidance, and suggestions for preparing this note.

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Discussion.

In a recent communication dated 11th November, 1948, to Dr. B. S. Chauhan, G. E. Gates has made the following observation.

....There are very many interesting looking localities as one goes by train from Allahabad to Calcutta that might well repay collecting. In particular where there are hills even though only low. Going north from Jubbulpore one got certain definite kinds of earthworms almost to the very limits of the plains, even when the altitude was a little over thousand feet. Some worms must have gotten in the past from the Assam area to the Central India area or *vice versa* and it would be very interesting to have more data on the worms from the ridges that run between those two areas....

ZOOGEOGRAPHICAL OBSERVATIONS ON THE FAUNA OF PARESNATH HILL.

By Sunder Lal Hora, *D.Sc.*, *F.R.S.E.*, *F.Z.S.*, *F.R.A.S.B.*, *F.N.I.*, *Director*, *Zoological Survey of India, Calcutta.*

Paresnath Hill in the district of Hazaribagh is the highest mountain in Chota Nagpur and its fauna is, therefore, of special significance in any discussion of the Satpura Hypothesis. The mountain rises to a height of 4,800 feet above sea-level and is about 180 miles from the foot-hills of Nepal. Its flanks and crest are covered with dense jungle and though the humidity is not as high as in the Eastern Himalayas, the atmosphere is damper in higher parts than the surrounding country. The mountain-top presents a mixture, in fairly balanced proportions, of the plants of a damp hot, a dry hot, and of a temperate climate.

The fauna of Paresnath had received little attention, till in April and May 1909, J. Travis Jenkins and N. Annandale made a small collection and reported the results (Jenkins 1910; Annandale 1912). In summarizing the results, Annandale came to the conclusion that

> 'Whereas a large proportion of the fauna of Paresnath is identical with that of the Ganges valley and a smaller proportion apparently endemic on the hill, a Himalayan element can also be detected which is totally absent from the surrounding plains.'

The Himalayan element in the fauna is represented by such forms as *Phlebotomus major* and *Sepsis cynipsea* among the Diptera, *Haphsa nicomache* among the Rhynchota, *Thysia wallichii* among the beetles, and *Lygosoma sikkimense* among the lizards. To these may be added a loach-like cat-fish, *Amblyceps mangois*, reported from the Hazaribagh district by Das (1939). In explaining the occurrence of Himalayan forms on Paresnath Hill, Annandale has remarked:

> 'Although winged insects might be blown with comparative ease across the Ganges valley from the Nepal foot-hills to Paresnath, it is quite impossible that a lizard could be carried in this way. It is impossible, moreover, that the eggs of *L. sikkimense* could be transported in a living condition by birds, for they perish within a short period of being removed from the damp moss in which they are laid. We must therefore seek for a geographical explanation of the occurrence of the lizard on an isolated hill-top two hundred miles from its present abode.'

Annandale has then discussed the various views advanced by geologists to account for such isolated occurrences on the hills of Peninsular India and made particular reference to the Glaciation theory. He has concluded:

> 'There is no reason whatsoever to think that the individuals living on Paresnath were ever isolated by a ring of ice or driven to the summit by glaciers sufficiently extensive to submerge the base of the hill; but it must be remembered that the secular movements of glaciers are accompanied by profound modifications not only in temperature but also in humidity, and humidity is perhaps an even more important factor in the distribution of reptiles and insects than actual temperature. We must suppose that *Lygosoma sikkimense* once lived in the plains as well as or instead of in the hills, but that a fall in the atmospheric humidity of the former, perhaps due in part to movements of glaciers in the Himalayas, drove it up into the E. Himalayas on the one hand and the summit of Paresnath on the other, or confined it to comparatively high altitudes.'

Smith (1936, p. 303) has included the Paresnath specimens described by Stoliczka as *Mocoa sacra* under *Leiolopisma* (= *Lygosoma* Blgr.) *Sikkimense* and has observed:

> 'The types of *Mocoa sacra*, two in number, differ from the typical form in having a more slender build and paler colouration. They may as well be retained under *sikkimense*.

Paresnath Hill, whence they came, is distant from the nearest Himalayan foot-hills by some 180 miles, and the occurrence of this strictly montane species south of the Gangetic Plain raises an interesting point in zoological distribution.'

Smith's observations make it clear that if more materials become available from the Paresnath Hill, it is likely that racial differences may be found constant between the Paresnath form and the typical form from the Himalayas, indicating thereby that isolation between the two forms probably occurred in the post-glacial period about 20,000 to 25,000 years ago. The second point is that isolation has not been the result of any fortuitous occurrence but is due to some palaeogeographical factors.

It is quite true that during the period of glaciation of the Himalayas, the atmosphere was damper in the plains of India but even then the dampness in the plains at sea-level could not have been of the same kind as it is to be found now either in the Eastern Himalayas or at the summit of the Paresnath Hill. For the migration of this lizard, as well as of *Amblyceps*, a continuity of low ranges of hills between the foot-hills of Nepal and the Paresnath Hill seems almost a necessity. In the Darjeeling district and in many parts of Sikkim and Eastern Nepal, *L. sikkimense* is found between 3,000 and 10,000 feet altitude, so besides humidity it would seem that temperature has been also a factor governing its distribution. The Satpura Hypothesis, therefore, fits in very well to account for the discontinuous distribution of this lizard and for the loach-like cat-fish *Amblyceps*.

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Vol. XVII, No. 6, 1951.

SOME OBSERVATIONS ON THE PALAEOGEOGRAPHY OF THE GARO-RAJMAHAL GAP AS EVIDENCED BY THE DISTRIBUTION OF MALAYAN FAUNA AND FLORA TO PENINSULAR INDIA.

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SOME OBSERVATIONS ON THE PALAEOGEOGRAPHY OF THE GARO-RAJMAHAL GAP AS EVIDENCED BY THE DISTRIBUTION OF MALAYAN FAUNA AND FLORA TO PENINSULAR INDIA.

By SUNDER LAL HORA, *D.Sc., F.R.S.E., C.M.Z.S., M.I.Biol., F.A.S., F.N.I., Director, Zoological Survey of India, Indian Museum, Calcutta.*

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CONTENTS.

INTRODUCTION.

After going through the Symposium on 'Satpura Hypothesis of the distribution of Malayan Fauna and Flora to Peninsular India' (Hora *et al.*, 1949), Dr. Ernst Mayr very kindly favoured me with the following comments:—

'Three points seem important:

(1) In view of the fact that the geological evidence for the recent date of the Garo-Rajmahal gap is very ambiguous, it is important to look for ecological factors that might have permitted transgap dispersal. Are the torrential fishes limited by oxygen in the water or by temperature or by absence of enemies? All three conditions might have been very different (in the low lands) at the height of the pluvial period.

(2) In order to determine the length of the immigration period (from Assam to the Nilgiris) as well as the possible number of such periods, it is important to analyse and tabulate the taxonomic status of the Nilgiri isolates. What percentage is generically, specifically, subspecifically different? What percentage are still identical (taxonomically) with the Assam-Himalayan population? Obviously, rates of evolution are not the same in all genera, but such a tabulation would permit an approximation.

(3) More attention should be paid to the eastern prong of colonization, going south through Bastar and the Eastern Ghats.

You have discovered a fascinating problem and I hope that your efforts for a final and complete solution will yield abundant results.'

In a recent review of the Symposium, Mayr (1950, p. 363) again referred to the significance of the Garo-Rajmahal Gap and stated:

'The geological evidence is ambiguous and seems to indicate a greater age for the Garo-Rajmahal Gap than postulated by Hora, although some geologists place it in the Pleistocene. Full agreement, however, exists in regard to the fact that during the Pleistocene the temperature was lower and the rainfall along these hills ranged much higher than is at present. The Zoogeographical importance of these hills is thus established, but whether or not complete continuity existed or was ever necessary remains to be determined. Throughout the Symposium little attention is paid to the possibility that animals can "jump" across considerable stretches of unsuitable terrain.'

In view of the considerations advanced above by Dr. E. Mayr, it seems necessary to re-examine the palaeogeography of the Garo-Rajmahal Gap from the late Pliocene to the end of the Pleistocene period. Except in the case of fishes, where three genera and two subgenera are different from the allied forms found in the Malayan Region, the Malayan isolates of other groups of animals found in the Peninsula have not

diverged generically or even subgenerically from the parental stocks. It can safely be assumed, therefore, that the bulk of this fauna migrated during the Pleistocene. The various levels of evolutionary divergences, ranging from endemic species to subspecific identity in the case of fish fauna are now under investigation by Mr. E. G. Silas. The question of the Eastern Ghats and the Orissa Hills as an alternate route of migration has been examined by Mr. A. G. K. Menon and a separate communication will appear on this subject shortly (*Proc. Nat. Inst. Sci. India*, in press).

Climatic Fluctuations during the Pleistocene.

Peninsular India was not glaciated during the Pleistocene, nor the glaciers came anywhere close to it. However, it underwent climatic fluctuations alternating with the pluvial and arid periods. Along with temperature changes, the glacial ages were moist with intensified precipitation and interglacial periods were dry on account of lessened precipitation. The pluvial periods thus favoured the growth of thick forests even in the plains and made the dispersal of the moisture-loving forms possible over vast tracts of the country. Such conditions were more characteristic of the higher elevations and persisted at suitable altitudes even during the inter-glacial periods. This would account for the occurrence of the terrestrial Malayan fauna and flora on the tops of isolated hills of the Peninsula even today.

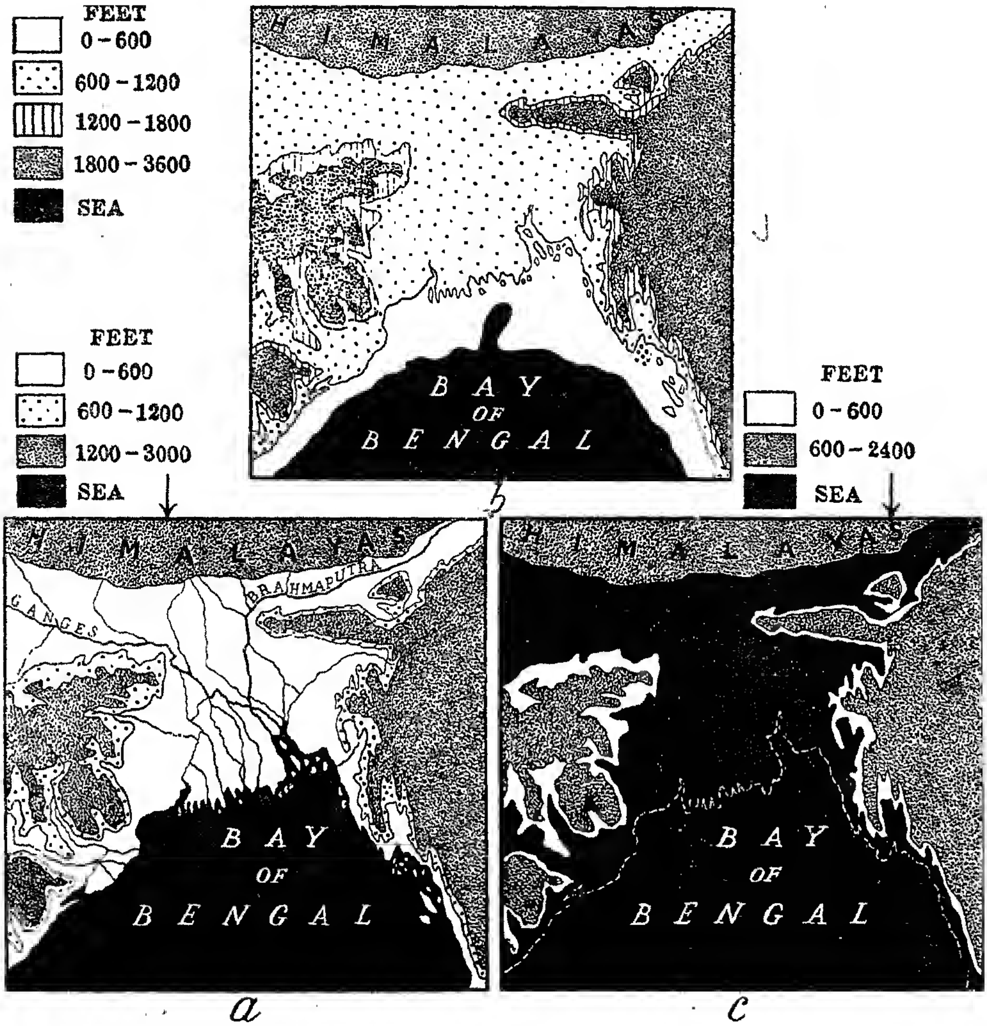
Under these conditions, during the pluvial periods, the terrestrial forms, like mammals, birds, etc., could have a very wide continuous distribution; but the same climatic conditions could not account for the dispersal of fishes and other aquatic fauna. There is no doubt that intensified precipitation produced more perennial streams and colder waters, containing more dissolved oxygen, were favourable for the life of torrential fishes. Rocky substratum is, however, necessary for their feeding, for their mouth parts are adapted for rasping off algal and other organic matter from rocks by applying their ventral surface very closely to them. During floods, the young of torrential fishes are sometimes washed down to the lower reaches of the rivers, but unless favourable ecological conditions are met with, they usually perish. Besides, for the dispersal of aquatic fauna, a continuity of water system is a very important factor and it is difficult to imagine how torrential fishes could ever have jumped across considerable stretches of unsuitable terrain. We have, therefore, to look for their dispersal not only a continuity of an elevated tract of country containing streams with rocky beds but also a mechanism for the commingling of waters of the streams in the east with those of the west, either through a series of river captures or tilting of drainage systems caused by earth movements.

Eustatic Movements during the Pleistocene.

'It is known that, since the beginning of the Pleistocene, the sea-level has undergone repeated fluctuations. These were chiefly due to the formation of large ice-caps in the higher latitudes, resulting in a drop in sea-level, and to the more or less complete melting of the ice during the interglacials and after the last Glaciation, resulting in high sea-levels. The high sea-levels of the earlier phases were higher than the present (as much as 100 m. in the Sicilian phase, earliest Pleistocene). The standard succession for the phases of high and low sea-levels has been worked out in the Mediterranean, but evidence shows that it applies also to other parts of the earth, including South Africa and Australia. One is justified, therefore, in assuming that the same or very similar levels apply to the Malay Archipelago, though local evidence is still scanty' (Zeuner, 1941, pp. 117-118).

Though no information is yet available on the fluctuations in sea-levels in the seas of India, presumably they were not too different from those found in the Malay Archipelago. A good deal of work on ancient shore-lines has been done in the Pacific (Stearns, 1945; Cotton, 1947), but since it is assumed that much of this up and down of oceans is a worldwide phenomenon, the results may be equally applicable to the Indian Ocean.

In the accompanying diagram, I have shown in fig. *a* the present-day orographic features of the Garo-Rajmahal Gap and of the adjoining country; the same during a glacial age (fig. *b*) when the sea-level is supposed to have fallen by 600 feet; and the same during the interglacial period (fig. *c*) when the sea-level is supposed to have arisen by 600 feet. Lines of 600 feet rise or fall have been used, as lines of



Orographic features of the Garo-Rajmahal Gap.
a. Present-day condition; *b*. Condition during a glacial period (hypothetical); *c*. Condition during a much warmer interglacial period (hypothetical).

lesser elevation or depth are not at present available. These maps are purely hypothetical and do not in any way represent the actual eustatic movements of the Bay of Bengal. From what has been observed elsewhere in the world, these maps may approximate the actual conditions, provided tectonic movements had not interfered with them otherwise.

Figure *b* shows two features which are of great importance for ichthyogeography of this region. The main branch of the Ganges, which is now definitely shifting eastwards, in flowing over the new land exposed during glaciation, probably had a more westerly course and may have joined the Mahanadi and the latter may have some of its branches confluent with those of the Godavari. This would mean a similarity between the fish fauna of the lower reaches of the Ganges, the Mahanadi and the Godavari. In fact, this is so, as nearly 90 % of the fauna of the Mahanadi is Gangetic in origin and 30 % of the Godavari is allied to the Mahanadi fauna. But this migration of the fauna has not affected the hill-stream species as Mr. A. G. K. Menon has not found any Malayan element in the fish-fauna of the Mahanadi. A full account of this zoogeographical fact will be found in Mr. Menon's article referred to above.

The second important fact is that the present-day Gangetic Plain was 600 ft. higher than its present level. Relative to the glacial sea, the area of the Garo-Rajmahal Gap then became a plateau and hill-streams must have flowed over it. The precipitation would have increased and a thick forest must have covered this area. In fact, the conditions would have been similar to what they are today in the foot-hills of the Eastern Himalayas and it is likely that without any continuity of the Garo and Rajmahal Hills, this tableland, with its torrential streams, may have permitted the dispersal of hill-stream fishes across the present-day Garo-Rajmahal Gap.

Now let us consider figure *c* in which the lowlying areas of Bengal and of the Brahmaputra and the Ganges Valleys are shown as submerged during the interglacials. Unfortunately we have no evidence of such submergence, for if any existed it now lies buried deep under the alluvium. So far as Calcutta proper is concerned, in digging for the foundations of Gillander House in Clive Street, at a depth of 5 to 6 feet, an old oyster-bed was discovered. Dr. H. C. Ray, Malacologist of the Zoological Survey of India, has very kindly drawn up the following table for me showing the type of shells that were taken out, their distribution and habits.

Table showing species of Molluscs taken from the Oyster-bed below Clive Street, Calcutta.

NAME.	DISTRIBUTION.	HABITS.
1. *Ostrea gryphoides* (Schlotheim).	(*a*) Originally known from the Tertiary deposits of Siebenburgen in the province of Austria. But subsequently recorded from the Tertiaries of other countries, namely, Mount Laberon in Central France, Germany, Portugal, Spain, Algeria, Crete Island, neighbourhood of Tarsus in Asia Minor, Virginia, Torino. If Lamarck's *O. canadensis* from the Atlantic coast of north-east America is considered to be identical with it, as stated by Preston, Smith and Annandale, then its range would also extend further. (*b*) First instance of geological occurrence in India was recorded by Mr. Murray	Large living specimens of oysters, according to Major A. W. Alcock, F.R.S., are found in large numbers in the mud banks near the mouth of the channels of the Sunderbans. Their peculiarly elongated umbonal part and the ligamental pit enable the animals to raise their shells above the mud in which they would otherwise be buried. He also adds: 'Judging from their large size and robust appearance, it is improbable that these shells could have flourished much above low water mark, implying a relative position of the sea and land decidedly different from that obtaining at present.' In the Clive Street excavations the shells were found in a soil of sandy loam and mud.

NAME.	DISTRIBUTION.	HABITS.
	Stuart in sandstones overlying the Kama clay in the Henzada district of Burma. (c) Discovery of large shells of this fossil species in the excavations at Clive Street, Calcutta, certainly marks the survival of Miocene Oyster in recent seas. The existence of similar shells, however, in a living state in the Sunderban areas also lends strong support to this view. Besides these, there are shells of the same species in the Museum Collection from Mergui, Penang and Cutch. So, judging from these evidences of distribution of *O. gryphoides* in the far south-east Asia, one may possibly pin some faith in the prediction made by De Joubert (a foremost worker, 1774–1777, on the Tertiary Oysters of the Mediterranean countries representing Lamarck's *O. crassissima* and *gryphoides*, 1819) that 'their living analogues were to be found in the seas of the East Indies.'	
2. *Telescopium telescopium* (Linn.).	Mangrove swamps on the coasts of India, Gangetic delta, Irrawaddy delta, Reunion, Madagascar, Ceylon, Malay Archipelago, Singapore, Nicobars, Java, Sumatra, Timor, Madura, Celebes, New Guinea, Nias, Pulo-Panjang, Australia, Philippines, Japan. Round the environs of Calcutta, it is found quite common in ditches.	It is essentially an estuarine form. The ponderous nature of its trochiform shell makes the animal usually more sluggish in disposition, somewhat-like *Mitra mitra* (Linn.).
3. *Indoplanorbis exustus* (Deshayes).	Commonest of the large Planorbids of Indian fresh waters, having its range extended into the plains of India and Burma. Records are also known from Siam, Malay Peninsula, French Indo-China and Sumatra. It can also live in brackish water containing negligible percentage of salt.	It is usually found in fresh water tanks, pools, canals, etc., attached to aquatic vegetation and fallen leaves, etc. It can also endure brackish water containing more than about 1% of saline residue. During the floods in July, 1907, Annandale found this species migrating into certain brackish ponds at Port Canning on the River Matla (Ganges delta) from which it was usually absent. But when the salt became concentrated after the evaporation of water, these animals were found completely disappearing from these ponds.

NAME.	DISTRIBUTION.	HABITS.
4. *Pila globosa* (Swainson).	One of the commonest freshwater molluscs, like *Viviparus bengalensis* (Lamarck), in Lower Bengal. But its range also extends to Orissa, Central Provinces, Rajputana and Bombay on the one hand and Bihar to United Provinces of Agra and Oudh on the other hand. It has not been known to occur in the Punjab, Sind, Madras and Burma. In the Punjab and Sind no living Pilid is found at the present day, while in Madras and Burma the species is replaced by *virens, conica* and *theobaldi*.	This common Indian apple-snail is usually found floating on the surface of water among aquatic vegetation. It is not known to have been found in brackish water.
5. *Viviparus bengalensis* (Lamarck).	Widely distributed in fresh waters of Lower Bengal. Its range also extends to Bihar.	This well-known banded snail occurs in large numbers in freshwater tanks, pools, lakes, etc., which are very rich in aquatic vegetation and having muddy bottom. It is also known to occur in slightly brackish waters near Calcutta.
6. *Anomia achaeus* (Gray).	A common species in the estuaries of the Ganges. But its wide range also extends to the Persian Gulf, Aden, Karachi, Bombay, Madras, Ceylon, Calcutta, Penang, Malacca, Kawa Bay and Amboina Anchorage.	This species is also often found in water that contains a sufficiently small proportion of salt to be called brackish.
7. *Monetaria moneta* (Linnaeus).	This money-cowry, as it has been commonly called, is essentially marine, being an inhabitant of clean salt water. Annandale writes: 'As, however, its shell was at one time used as money in Lower Bengal, its presence in the deposit at Clive Street, Calcutta, may be purely adventitious.' But its wide range extends from the Gulf of Oman and Strait of Hormuz, Red Sea on the west as far as Arakan on the east. Recently Abbott has recorded this species from the Cocos-Keeling Islands.	This well-known species occurs in the shallow waters of the sea, mostly in the coral reef areas.
8. *Ostrea cucullata* (Born).	This is a common brackish water species found widely distributed in the Indian Ocean, Gulf of Suez, Gulf of Aden, Red Sea, Bombay, Mada-	The species is found fixed on shells, stones, etc., encrusting the rocks below high- and low-water levels. It is also found on sand below mangrove trees.

Name.	Distribution.	Habits.
	gascar, Mozambique, Ceylon, Madras, Lake Chilka, Elphinstone Island Bay, Siam, Sumatra, Timor, Moluccas, Australia, Philippines, Japan. Dr. Annandale found this species in abundance in the Matla River, Port Canning, where the water contained only 2·5% of saline residue.	

The 8 species of molluscs recorded in the table show that, when this bed was formed, estuarine conditions prevailed over the Calcutta area. Purely fresh water forms, *Indoplanorbis exustus*, *Pila globosa* and *Viviparus bengalensis*, may have been washed down from the neighbouring brackish or freshwater marshes.

Unless borings are taken in a number of places in the area of the Gap, it is difficult to say with certainty as to what happened during the interglacial periods in regard to the rise of the level of the sea. If there were no high ridges between the Garo and the Rajmahal Hills and if the sea-level had arisen as postulated here, considerable portions of the Ganges and the Brahmaputra valleys must have been submerged as shown in the figure.

Professor E. F. Zeuner was consulted with regard to the eustatic fluctuations in the Bay of Bengal and their likely effect on the Bengal Gap. He very kindly wrote to say that:

> '1. It is true that if conditions on land had remained entirely stable the lowlying areas of Bengal would have been submerged in the interglacials. Evidence for such short period submergence of flat country is very rare because the shallow deposits formed are very rapidly incorporated in the weathering soil forming after the following regression. They disappear, therefore, in most places in a very short time.
>
> 2. There is, however, the possibility that the Ganges depression is an area of continuous tectonic subsidence, *i.e.* it is possible that the sinking has continued, throughout the late Tertiary and Pleistocene and more or less kept pace in the filling process. In this case the gap was not necessarily inundated in high sea-level times. Since both alternatives are reasonable and there is no evidence proving that one of the two is false, it is impossible to have a definite opinion regarding your point.'

Van Bemmelen in his 'Geology of Indonesia' (p. 97) has also sounded a similar warning. He states:

> 'It appears from these critical remarks that it is a quite hazardous enterprise to try to correlate the Pleistocene stages of the orogenic belts of the Indian Archipelago with eustatic movements caused by fluctuations of the pleistocene glaciation.'

Dr. J. B. Auden has pointed out to me that along the mobile orogenic belts, in the most recent of which tectonic movements are still taking place, the changes in elevation due to orogenic forces may be far in excess of any possible change due to eustatic movements of sea-level, which are likely to have been of the order of 70 to 100 metres. Even in the now relatively stable peninsula of India, it is likely that broad warps are taking place, and have taken place, some going counter to the particular eustatic trend of the sea at the moment, and some of the same sign as the eustatic movement.

From the above discussion it will be seen that though it may be difficult to prove the submergence of the Gap area during the interglacials, there is enough evidence of the fall of the sea-level in the fish fauna of the Mahanadi and the Godavari and a

relative rise in the altitude of the Gap area with consequent heavier precipitation and formation of torrential streams in the region.

Summary and Conclusions.

In reviewing the Satpura Hypothesis (1950, p. 368-369), for the first time attention was paid to the relative height of the Garo-Rajmahal Gap during the glacial periods and its suitability for the dispersal of mountain species. In the Satpura Hypothesis, the main difficulty was to find out some means by which hill-stream fishes could spread from the Garo Hills to the Rajmahal Hills and hitherto attempt has been made to fill up the gap. Now it is postulated that a eustatic drop in the sea-level of 600 feet is likely to have had the same effect, both climatically and topographically. During each glacial age, favourable conditions for dispersal were established and thus waves of migration can now be dated to correspond with the Glacial Ages of the Pleistocene.

It is perhaps necessary to point out here that the river Ganges in its present form came into existence in the late Pleistocene, may be just before the last glacial epoch, and could not, therefore, have acted as a barrier for the dispersal of small torrential fishes. During the last Glacial period, parts of the Gangetic fauna probably became transferred to the Mahanadi over the newly exposed land.

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DAVID STARR JORDAN CENTENNIAL NUMBER

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DAVID STARR JORDAN, ICHTHYOLOGIST, 1851-1931

By George S. Myers

David Starr Jordan, greatest of American ichthyologists, became the first president of Stanford University upon its opening in 1891. This year, on the hundredth anniversary of his birth, it is fitting tnat Stanford ichthyologists should in some measure attempt to honor the memory of their leader by publication of a David Starr Jordan Centennial Number of the Stanford Ichthyological Bulletin. As the first article of this number, a brief sketch of Jordan's ichthyological career is offered by the writer, who was the very last of Jordan's many students.

David Starr Jordan was born on January 19, 1851, on a farm near Gainesville, in the western part of the state of New York. He grew to manhood in a country environment and, after completing secondary school, became a schoolteacher for a brief period. When he entered Cornell University in 1869 at the age of 18, Jordan tells us in his autobiography[1] that he was six feet tall and weighed 180 pounds. Throughout his life his great size and physical strength made him a commanding figure.

At Cornell, Jordan continued a boyhood interest in botany. Upon graduation in 1872, he accepted a professorship in natural science at Lombard College in Galesburg, Illinois, where he remained until the summer of 1873. At that time, Jordan was chosen as one of the students at the first session of the short-lived but famous summer school of natural history established by Louis Agassiz on Penikese Island, off New Bedford, Massachusetts. The teachers were Agassiz, Burt G. Wilder, Edward S. Morse, Alpheus S. Packard, Alfred Mayer, F. W. Putnam, Arnold Guyot and Count Louis de Pourtalès. Among the students were such men as W. K. Brooks, C. O. Whitman, F. H. Snow, C. S. Minot, Walter Faxon and Samuel Garman. At Penikese Jordan devoted himself to marine algae, but Agassiz asked him to undertake a study of the fishes of the region, and in examining the catches of the pound-nets at Marthas Vineyard, Jordan for the first time became well acquainted with fishes and their literature.

After the summer at Penikese, Jordan became professor in the Appleton Collegiate Institute, at Appleton, Wisconsin. Here, in the middlewest, marine algae were far away, and Jordan began study of the local fishes. Louis Agassiz had died, but Jordan returned to Penikese the next summer (1874) and in Massachusetts met George Brown Goode and others of the then newly established U.S. Fish Commission. That autumn Jordan accepted a teaching position in the high school at Indianapolis, Indiana, where one of his students was Charles Henry Gilbert, who was to be associated with Jordan for many years The summer of 1875 was spent in the Harvard Summer School of Geology in Tennessee and Jordan returned to Indianapolis as professor in Butler College. It was here, in 1875 and 1876, while living with H. E. Copeland, a fellow-student of Cornell days who had taken over Jordan's teaching position in the high school, that Jordan and Copeland decided to devote their research principally to ichthyology. The first of their papers concerned the "johnny darters" (Etheostomatinae), a catalogue of American fresh-water fishes, and a re-identification of Rafinesque's Ohio fishes. Copeland died in 1877 and Jordan carried on the ichthyological work alone.

[1] "The Days of a Man" (see reference at end). This autobiography is well known to Stanford men but appears to be relatively unknown to ichthyologists in general. It is a veritable mine of ichthyological history.

In 1876 appeared Jordan's "Manual of the Vertebrates of the Northern United States," an outgrowth of a previous "popular key" which had been published by Jordan and Van Vleck in 1874. The "Manual," of which 13 editions were published (the last in 1929) became the best known of all Jordan's publications and served an exceedingly useful purpose in North American zoölogy for nearly three generations.

In the summer of 1876, with Gilbert, Jordan set out for Georgia, on the first of many excursions afoot and by wagon to explore the fish-fauna of the southeastern states. Ichthyological papers now began flowing from Jordan's laboratory in a steady stream, with publication assured through Spencer Fullerton Baird of the Smithsonian Institution in Washington. Other students came to Butler to work with Jordan, among them W. A. Brayton and B. W. Evermann, and the collecting trips during the summer months continued.

By 1879, Jordan had become the most active American ichthyologist, and a respected friend and colleague of Baird, Gill, and Goode in Washington. That summer, and again in 1881 and 1883, Jordan and a group of students and friends went to Europe, where they travelled, mostly afoot, over large parts of England, Belgium, Holland, France, Germany, and Italy. In 1883 Jordan, Gilbert, and some others made the ascent of the Matterhorn; Gilbert was badly injured by a falling rock during the descent. On these European tours Jordan met many of the great ichthyologists of Europe, among them Albert Günther, C. F. Lütken, and L. Vaillant. In 1881 Günther attempted to induce Jordan to become his assistant in the British Museum. Shortly afterward, G. A. Boulenger accepted the position.

In the autumn of 1879, Jordan became professor of natural science in Indiana University, and transferred his activities (and many of his students) to Bloomington. Here the opportunities were much greater than at Butler, However, hardly had Jordan assumed his duties when Baird and Boode asked him to survey the fishes and fisheries of the Pacific Coast in connection with the production of Goode's immense work, "Fisheries and Fishery Industries of the United States." Jordan obtained leave and left for the west with Gilbert in December of 1879. In nine months they covered the coast from San Diego to Vancouver, Jordan stopping in Utah and elsewhere on the return trip to Indiana. The result was a long series of papers on the fishes of the Pacific Coast by Jordan and Gilbert, and their publication, in 1883, of a "Synopsis of the Fishes of North America," the first modern compendium on the subject.

Students flocked to Jordan's lectures, among them Gilbert, Carl H. Eigenmann, B. W. Evermann, C. H. Bollman, and Seth E. Meek, all to become well known in ichthyology. Gilbert collected in Panama; and summer trips to Europe, or to collect fishes in the southern states, continued. While in Paris in 1883, Jordan heard that Owen Hall at Indiana University had been destroyed by fire, and with it Jordan's library and collections, including the entire Panama collection and the manuscript on it. Jordan began to replace his ichthyological library at once, and further expeditions soon built up the collections. On a trip to Havana in 1884 Jordan became acquainted with Felipe Poey, the venerable ichthyologist of Cuba, who had been a student of Cuvier in Paris. In his later years, Jordan himself sometimes pointed out to his students that they were, intellectually, lineal descendants of Cuvier, for Agassiz had been a disciple of Cuvier, and Jordan of Agassiz. By 1890, Jordan had collected fishes in every considerable river basin in the United States, and on most of its coastline, as well as in Europe, Cuba, and Canada.

In January, 1885, Jordan became president of Indiana University, and from that time on a great deal of his energy was taken up with the larger duties of university administration. Jordan was active and brilliant, and under his administration the university grew and the faculty was greatly expanded and improved. Gilbert became professor of zoölogy. It is in-

teresting to note that one of Jordan's appointments, which failed to materialize, was of a young Norwegian zoölogist, Fridtjof Nansen, who declined the appointment in order to make an exploring trip across Greenland—and later became famous as an arctic explorer. Jordan also broadened the curriculum and established the system of free elective subjects for students, thus departing from the rigid system that had so notably retarded American university development. As a result he became widely known, not only as the youngest American university president, but also as perhaps the most forward-looking of all. He arranged for distinguished visitors to give lectures, among them Alfred Russel Wallace and Theodore Roosevelt, the latter being not only prominent in politics but also an enthusiastic naturalist. But Jordan contined to teach himself, and did not stop his ichthyological work. A trip to study the fishes of Greece was planned with Professor Hoffman of the Classics Department, but although Jordan was himself unable to go, Hoffman obtained enough material for a little catalog of Greek fishes by Jordan and Hoffman, the most important work on this fauna since the time of Aristotle.

When Senator and Mrs. Leland Stanford of California decided to found and endow a great new university in memory of their son Leland Stanford, Jr., their choice for a leader and president was David Starr Jordan. The university buildings were located on the Stanfords' "Palo Alto Stock Farm," about 30 miles south of San Francisco, between the Outer Coast Range and the southern arm of San Francisco Bay. Jordan himself selected most of the faculty, Gilbert being head of the Zoology Department and Oliver Peebles Jenkins professor of physiology. Ichthyology was, of course, not forgotten, for Jordan brought with him his large personal library and arranged for the transfer of half of the fish collection he had built up at Indiana University. Eigenmann at that time became professor of zoölogy at Indiana University. Stanford opened its doors to its first class in the autumn of 1891. Among the first ichthyological students to arrive at the new western university in the early 1890's were John Otterbein Snyder and Alvin Seale, both of whom came from Indiana, Seale riding most of the way across the continent on a new bicycle.

Stanford's early days were clouded not only with the growing pains of a new institution but also by a lawsuit which threatened the large endowment and very existence of the university. In spite of all this, Stanford at once assumed a leading position among American universities. And Jordan, against great odds, pushed rapidly to completion his *magnum opus*, "The Fishes of North and Middle America." This great work, published by the National Museum in 1896-1900, consisted of four thick volumes, in very fine type, comprising some 4,000 pages. Originally conceived as a joint work by Jordan and Gilbert and largely written by them, Gilbert became involved at Stanford in study of the deep-sea fishes being collected in the Pacific by the U.S.S. "Albatross" and resigned co-authorship. Evermann, by then ichthyologist of the U.S. Fish Commission in Washington, assumed what was essentially literary editorship, and became co-author in Gilbert's place. No other great regional work on fishes has ever been more extensive and better executed and has had, at the same time, so great an impact upon the ichthyology of the world as a whole as "Jordan and Evermann."

Nor was this work all that Jordan accomplished in the first decade at Stanford. He visited the west coast of Mexico with a group of students, and in rapid succession published "The Fishes of Mazatlan" and "The Fishes of Puget Sound." Jordan also visited Alaska as member of the International Fur Seal Commission, resulting in a large "Fishes of Bering Sea." Gilbert collected again in Panama and late in the decade Jordan and Snyder explored the fish fauna of central Mexico. And a young zoölogist from Seattle, Edwin Chapin Starks, came to Stanford as curator of the collections, to join Snyder, Seale, and the others.

In 1901, Jordan and Snyder made a long ichthyological expedition to Japan. The large collection resulting was worked up by groups, by Jordan in collaboration with different students (Snyder, Starks, A. W. C. T. Herre, H. W. Fowler, Michitaro Sindo, R. E. Richardson, and W. F. Thompson), the resulting papers forming the firm basis on which Japanese ichthyology will always rest. Other expeditions to Hawaii and to Samoa resulted in large monographs on the fish faunas of those islands by Jordan and Evermann, by Gilbert, and by Jordan and Seale. Other extensive memoirs on the fishes of Korea, of Formosa, and of Japan were also published, the last as a result of Jordan's second Japanese trip, in 1911. In 1907, Jordan visited Australia and New Zealand on a lecture tour, meeting and becoming a lifelong friend of the ichthyologists there, J. D. Ogilby, A. R. McCulloch, E. R. Waite, and D. G. Stead.

Jordan had become, by 1910, an important and honored national figure in the United States. He was one of the two or three best known university leaders in the country. His biological text-books were known everywhere. He had lectured widely on a favorite topic—the loss through war of the cream of a nation's manhood and the consequent adverse hereditary effect upon the nation—and had become one of the foremost international figures in the peace movement. Under university regulations, he was to retire in 1916, but, as war clouds gathered in Europe, a new and energetic member of the Stanford Board of Trustees, Herbert Hoover (who had already become internationally known as a mining engineer) suggested that Jordan retire at once to devote his energies to the cause of peace.

In June of 1913 Jordan resigned the active presidency of Stanford and assumed the title of Chancellor of the University. At the same time he ceased ichthyological work, naming what he thought would be his last "new species," a macrurid, *Coryphaenoides bona-nox*. He left immediately for Europe, visiting England, France, Belgium, Germany, Switzerland, Italy, and Montenegro, lecturing and consulting with statesmen, scientists, and plain people everywhere, in an effort to stem the militaristic tide. Jordan left Europe for Australia, early in 1914, stopping to collect fishes at Port Said, and returned to Europe after but a month's stay. He then visited Croatia, Hungary, Bulgaria, Roumania, Greece, and Turkey, also on peace missions. Thence he went to Paris, London, and Ireland, and was in England at the outbreak of the war. From England Jordan returned to the United States, greatly saddened by the holocaust in Europe.

The war years, and especially the entry of the United States in 1917, left Jordan with some free time and he again plunged into ichthyology. Two projects were carried on, one on fossil fishes recently found in California and the other on nomenclature of the genera of fishes of the world. The "Genera," published in four parts from 1917 to 1920, was followed by a general "Classification of Fishes" in 1923. In 1919, with a student of the war years, Carl Leavitt Hubbs, who later was to attain fame through his revisions of American fishes, Jordan reviewed the silversides. In 1922, Jordan visited Japan for the last time, and in 1925, with Hubbs, published his last memoir on Japanese fishes. From this time on, two works occupied most of Jordan's research time. One was a final (13th) edition of the "Manual of Vertebrates," the other a checklist of North American fishes, published in 1930 in collaboration with Evermann and H. W. Clark. Two of Jordan's greatest students, Gilbert at Stanford and Eigenmann at Indiana, died in 1927. Snyder was now head of the Zoölogy Department, Starks was a member of the faculty, and Herre was curator of the zoölogical museum. The writer studied first with Eigenmann, and was closely associated with Jordan from 1926 until his death.

Within a year or two of Jordan's death both Snyder and Starks had retired. Herre and Willis H. Rich at Stanford, and Rolf L. Bolin at the University's marine station, remained to carry on ichthyological work at Stan-

ford. The writer, who left Stanford in 1933 to undertake duties at the National Museum, returned in 1936.

It is quite impossible fully to estimate Jordan's far-reaching contribution to ichthyology. During most of his days he lived three distinct lives —that of a scientist, that of a teacher and university administrator, and that of a well-known public figure and exponent of international peace. His labors in all three were prodigious and would, in any one of them, have been sufficient to fill completely the life of a busy and able man. In ichthyology itself, a number of men have surpassed him in certain segments of the science, but none has ever approached him when the entire field is considered. He contributed heavily to general biological thought, but some of his best ideas were presented in text-books and lectures where later workers seldom look. Certainly, Jordan had the broadest human interests of any of the great ichthyologists. He left a continuing and indelible imprint on the ichthyology of the entire world, not least as teacher of the greatest school of disciples ichthyology has ever seen. Finally, to Stanford he bequeathed not only his great library and collections but also leadership in an important line of human endeavor.

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1922 The days of a man, being memories of a naturalist, teacher and minor prophet of democracy. Vol. 1, xxviii+710 pp.; Vol. 2, xxviii+906 pp., with many portraits and illustrations. World Book Co., Yonkers, New York. [Jordan's autobiography.]

MEADIA, A NEW GENUS FOR THE WEST PACIFIC DYSOMMID EEL, DYSOMMA ABYSSALE KAMOHARA.—For a new genus of dysommid eels, the name *Meadia* is here proposed, to contain at present only the generic type, *Dysomma abyssale* Kamohara. *Meadia abyssale* (Kamohara) is distinguished from the genus *Dysomma* on the basis of its very distinctive dentition. The dentition of *Dysomma* is as follows: upper jaw with a row or a band of tiny, sharp teeth; a row of large canines at the front end of the vomer; no teeth on palatines; a single row of small or medium-sized teeth on mandibles. The dentition of *Meadia abyssale* (according to Kamohara 1938, On the offshore bottom-fishes of Prov. Tosa, Shikoku, Japan, p. 12) consists, however, of: "maxillary with a band of villiform teeth on posterior two-thirds; several canines on anterior part of upper jaw; a single canine on vomer; about twelve canines on anterior part of palatines, nearly in two longitudinal rows, followed by about thirteen smaller ones in a series. A band of villiform teeth on either side of lower jaw, each with several canines anteriorly." Thus, the presence of canines anteriorly on the upper jaw and mandible, only a single canine on the vomer, villiform teeth on the lower jaw, and palatine teeth all serve to distinguish the genus *Meadia* from *Dysomma*.—J. Böhlke.

DYSOMMINA RUGOSA, AN APODAL FISH FROM THE NORTH ATLANTIC, REPRESENTING A DISTINCT FAMILY[1]

By James Böhlke and Carl L. Hubbs
Stanford University and Scripps Institution of Oceanography

The strange eel here considered was first described in manuscript by Hubbs in 1916, as part of a collaborative report with the late Dr. C. H. Gilbert. A recent re-examination of a specimen by Böhlke[2] brought the problem up again, resulting in a combination of the two independently written manuscripts. Just as our paper was going to press, with the species named for Dr. Jordan, a description of what appears to be the same form has been published by Ginsburg (1951). As our conclusions differ notably from his, our paper is allowed to stand almost unchanged except for the use of Ginsburg's names.

DYSOMMINA Ginsburg

Dysommina Ginsburg, 1951, p. 450 (type *D. rugosa* Ginsburg).

Body elongate, compressed, slender. Anus far in advance of mid-length. Scales absent, skin smooth. Lateral line indistinct, evidently beginning rather high on body anteriorly, descending to middle of tail. Eyes covered by a layer of skin, placed anterior to mouth angle. Snout long, rounded, projecting beyond the lower jaw, and covered, as the lips and lower jaw, by small papillae. Mouth cleft wide, horizontal, lateral. Anterior nostril tubular, near tip of snout; posterior nostril with flared rim, enlarged to form a flap anteriorly, lateral, immediately in advance of eye. Teeth small, sharp, in bands on maxillaries and mandibles; four or five large, conical, widely spaced teeth set in pockets on the shaft of the vomer. Branchial apertures crescentic, oblique to nearly horizontal, below pectoral base, well separated below. Dorsal commencing behind head, anal before mid-length of body and immediately behind anus. Caudal well developed, pointed, confluent with dorsal and anal fins. Membranes of vertical fins thick. About 16 brancniostegals.

Frontals and parietals paired. Mesetnmoid a thin V-shaped element, shaped like a tear-drop in cross-section, fused with vomer. Pterygoid bones everywhere reduced to thin splints. Prootic thin, little flattened anteriorly, expanding into a bulb posterodorsally. Maxillaries and mandibles long and thin, bearing wide bands of teeth. Hyomandibular one of the largest bones, composed of a strong ridge and supporting shelves that are equal in width to the wide head of the bone. Opercle elongate and low, originating on lower one-half of hyomandibular. Basioccipital-vomerine axis virtually straight. About 13-16 rudimentary gill rakers on lower limb of first arch. Slit behind fourth gill reduced to about one-half length of lower first gill arch.

[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 525.

[2] The kindness of Doctors Alexander Wetmore and Leonard P. Schultz of the National Museum has now permitted the permanent retention of one example at Stanford.

Dysommina rugosa Ginsburg

Dysommina rugosa Ginsburg, 1951, p. 450 (Albatross Station 2667, off Cumberland Id., Georgia).

Two examples: USNM 44324, collected with large beam trawl by the U.S. Fish Commission Steamer "Albatross" in the Gulf Stream off southern Georgia, at Station 2669, 31°09'00" North Latitude, 79°33'30" West Longitude; May 5, 1886; depth 352 fathoms; bottom temperature 43.7°F.; bottom recorded as gray sand and dead coral. SU 24284, 215 mm. in total length, collected with the previous example.

Description: Measurements of no. 44324 in mm.: total length 289, head length to anterior end of gill opening 41.5 (.14 of standard length), tip of snout to dorsal origin 56 (.19 of standard length), tip of snout to anal origin 89 (.31 of standard length), greatest body depth 21, length of snout 15, eye diameter 4, fleshy interorbital width 7, gape 22, pectoral fin length 7, longest caudal fin rays 8.

Head and trunk contained just over three times in total length. Greatest depth of body 2.0 (1.9)[3] in length of head, 13.8 (14.3) in total length. Head 7.0 (7.4) in total length. Eye diameter contained 10.4 (9.7) in head length, 1.8 (No 24284 damaged) in interorbital width. Snout length 2.8 (2.9) in length of head, 19.3 (21.5) in total length. Gape extending slightly less than an eye diameter beyond eye, its length 1.9 (2.0) in head length.

Maxillary teeth in 4 or 5 wavy, irregular rows; those on mandibles similar, in bands which are widest anteriorly. Vomerine teeth consist of 4 or 5 much enlarged canines (posterior one lost from no. 24284), widely separated, set in individual pockets on the shaft of the vomer, their bases enclosed in the folds of skin which line the roof of the mouth much as in some of the dysommids. In fact, with the exception of the pair of anterior vomerine teeth which are present in *Dysomma anguillare* Barnard and absent in this new species, the entire dentition in the upper jaws of these fishes is strikingly similar. Tongue adnate. Postorbital region of head supported by the branchiostegals, some of which are visible through the skin of the branchial region.

Dorsal fin commencing posterior to tips of appressed pectorals, continuous, the distance from the tip of the snout to its origin contained 5.2 (5.2) in the total length. Distance from tip of snout to anal origin 3.2 (3.2) in total length. Vertical fins confluent around end of tail, the tip pointed; longest caudal rays 5.2 (4.3) in length of head. Small pectorals covered by rather heavy skin, their length 5.8 (5.3) in head length, 41.3 (39.1) in total length.

Pores not obvious in the lateral line proper. The only conspicuous pores in the lateral line system of the head are the elongate, open pores of the mandibular series, 4 very obvious pores in the infraorbital series (posterior to the anterior nostrils), and a single pore just posterior and median to either anterior nostril.

Color in alcohol uniformly light tan, with small groups of melanophores more or less evenly spaced along mid-line of body. Peritoneum black.

Relationships: Ginsburg's genus cannot properly be placed in any of the described eel families as currently defined (Regan 1912, p. 379; Trewavas 1932, p. 656). In external appearance and tooth pattern this genus bears a strong resemblance to several of the dysommids, but its enlarged otic bulla and paired frontals in particular are characters which would place it near the Heterenchelidae, Moringuidae, and the genus *Kaupichthys* (see Gosline 1950, p. 313). It resembles the Moringuidae in having the palatopterygoid reduced to a splint and the vomer ankylosed with the ethmoid; it differs

[3] **Proportions for no. 24284 in parentheses.**

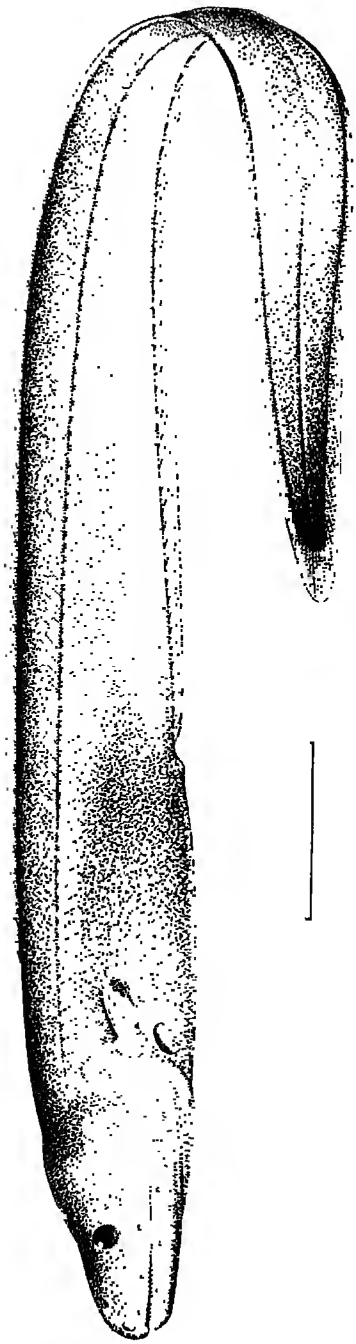

FIG. 1. *Dysommina rugosa* Ginsburg. USNM no. 44324. (Drawn by the late William Sackston Atkinson. Reproduced from a photo of the original drawing in the files of the Division of Fishes, U. S. National Museum.) Line represents one inch.

from that family, however, in having the tail much longer than the trunk, vertical fins that are not confined to the tail, and bands of teeth on the maxillaries and mandibles (versus uniserial on mandibles and uniserial or absent on maxillaries). Ginsburg's genus resembles the Heterenchelidae in having the tail much longer than the trunk, but differs trenchantly from that family in having the vomer ankylosed with the ethmoid rather than being separated by a suture, and the palatopterygoid reduced to a splint rather than being well developed and laminar. The new genus resembles *Kaupichthys* in having the trunk shorter than the tail and in lacking a suture between ethmoid and vomer. It differs from that genus, however, in having the posterior nostrils lateral rather than labial and tubular, in having the palatopterygoid reduced to a thin splint rather than well developed and laminar, and in the different character and shape of the branchial openings.

On the basis of the characters indicated above and by reason of its very distinctive external appearance, *Dysommina* should stand, at least provisionally, as the type of a distinct family of apodal fishes, the Dysomminidae.

Thanks for assistance in the study of this new eel go to the late Dr. Charles Henry Gilbert, who long ago placed the old "Albatross" collections in Hubbs' hands for a collaborative report that remains in manuscript; to Dr. Leonard P. Schultz of the National Museum, for the loan of the specimen and the accompanying illustration; to Mr. Norman J. Wilimovsky of Stanford University, for assistance in the osteological preparation; and to Dr. George S. Myers of Stanford, for advice throughout.

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FRESH-WATER FISHES AND EAST INDIAN ZOÖGEOGRAPHY[1]

By George S. Myers

1. Introduction

In a paper published over a decade ago, the writer noted that zoögeographers, like Gaul, are divided into three parts—those who build bridges, those who do not, and the proponents of continental drift. This is still true, but it may be remarked that the thinning ranks of the bridge-builders and the drifters are today almost deserted by the zoölogists. Some of the old-line botanists still stoutly man the Wegenerian or Gregorian ramparts, and conduct isolated sorties for the glory of drift or a foundered Pacific continent, but they are scarcely aware of the strength mustered against them.[2] My purpose is to fire one more gun against these besieged garrisons, and, at the same time, to point out what modern fresh-water fish evidence appears to indicate in regard to the history of the Pacific island groups, especially the East Indian or Malay Archipelago.

Only recently have fresh-water fishes come into their own in interpreting continental zoögeography. In the time of Darwin and Wallace they were too little known to be of great importance, and most of the main strokes in the zoögeographical picture were painted from the evidence of mammals and birds. Eigenmann (1909) and Regan (1922) were the pioneers in modern ichthyological geography, but their belief in a great late Cretaceous South Atlantic land bridge, like that of others in a great Pacific continent, has gradually been discarded, simply because it creates far more problems than it solves. In regard to such bridges, I wish to quote from a well-known British naturalist, as follows:

"Ingenious men will readily advance plausible arguments to support whatever theory they shall choose to maintain; but then the misfortune is, everyone's hypothesis is each as good as another's, since they are all founded on conjecture. The later writers of this sort, in whom may be seen all the arguments of those that have gone before.....stock America from the western coast of Africa.....and then break down the Isthmus that bridged over the Atlantic. But this is making use of a violent piece of machinery; it is difficulty worthy of the interposition of a god! '*Incredulus odi.*'"

Some of you may recognize the quotation. It occurs in a letter to Thomas Pennant, written by Gilbert White, at Selborne, May 29th, 1769 (see White, 1788). Vast continental land bridges have been opposed by some naturalists for a very long time!

As recently as 1938, I pointed out for the first time that the so-called true fresh-water fishes, which alone have been recognized as good evidence in terrestrial zoögeography, really consist of two groups, a primary one composed of fish families sharply restricted to fresh water and a secondary of families which apparently are able to cross short ocean barriers. The primary fresh-water fishes were shown to be sharply restricted to the continents, whilst the secondary alone have been able to reach the Greater Antilles, Madagascar, and other peripheral areas. In 1948, Darlington gave an excellent resume of the world's fresh-water fish distribution, in which he expanded the fish data given in my 1938 paper, and included amphibians,

[1] Presented by the author 1th February 1949 at the Seventh Pacific Science Congress, in New Zealand, under the title: Paleogeographical significance of fresh-water fish distribution in the Pacific.

[2] See especially Matthew, 1915, 1939; Noble, 1925; Dunn, 1931; Schmidt, 1943; Simpson, 1939, 1940, 1941, 1943; Darlington, 1948; Berry, 1928; Chaney, 1940.

and reptiles as well. Darlington gave only brief attention to the Pacific island faunas, but a familiarity with his paper is necessary in interpreting fresh-water fish distribution. If we then add some interesting discussions by Nichols (listed by Darlington, 1948), this completes the main recent history of general fresh-water fish geography, unless one wishes to include such compilations as those of Meek (1916), Kyle (1926), MacFarlane (1923), Scheuring (1929, 1930), and Arldt (1938). The last is, I believe, the most ponderous existing example of the way biogeography should *not* be done.

2. Fresh-water Fishes

The fishes of fresh waters may be classified zoögeographically in the following groups (Myers, 1938, 1949):

1. **Primary.** Strictly intolerant of salt sea water. (Existing Dipnoi, Polypteridae, Osteoglossidae, Cyprinidae, Characidae; most families of siluroids; Centrarchidae, Percidae, etc. There are a few exceptions in these groups, but they are exceedingly few.)
2. **Secondary.** Rather strictly confined to fresh water but evidently capable of occasionally crossing narrow sea barriers; tolerance of sea water for short periods known for many. (Lepisosteidae; most Cyprinodontidae, Poeciliidae and Cichlidae; Synbranchidae, etc.)
3. **Diadromous.** Fishes which regularly migrate between fresh and salt water at a definite period of the life cycle. (Sea-lampreys, *Alosa, Oncorhynchus, Galaxias, Anguilla, Sicydium,* etc., etc.)
4. **Vicarious.** Presumably *nondiadromous* fresh-water representatives of partly or primarily marine groups. (*Siniperca; Lota; Plagioscion;* fresh-water Ariidae, Plotosidae, Apogonidae, Atherinidae, and Syngnathidae; land-locked or nondiadromous Galaxiidae; etc.)
5. **Complementary.** Fresh-water fishes, often or usually diadromous and belonging to marine groups which become dominant in fresh water only in the paucity or absence of primary, secondary, and probably also vicarious fresh-water faunas. (*Agonostomus, Joturus, Cestraeus, Sicydium, Sicyopterus, Stiphodon,* certain New World Gobiesocidae, etc.)
6. **Sporadic.** Fishes which live and breed indifferently in salt or fresh water or which enter fresh water only sporadically and not as a part of a true migration. (Many Lutianidae and Sciaenidae; probably many Mugilidae; *Gasterosteus, Mollienisia,* etc.)

The continental fish faunas of the world are composed principally of primary fresh-water fishes, amd most of the remainder are secondary fresh-water fishes. The families of the primary group appear mostly to have had a long fresh-water history, extending back to the Eocene, and their physiological intolerance of sea water seems to be deep-seated (Myers, 1938).

True fresh-water fishes seldom cross ocean barriers; those of the primary group almost never do but the secondary ones appear to have done so on several occasions. Fishes of the vicarious group may often be able to make such crossings, since most of them appear to be of relatively recent derivation from marine types. If they are purely fresh-water residents of relatively long standing, they may show geographical relationships between lands now separated by the sea. But each instance of this type must be closely judged on its own merits. Diadromous, complementary and sporadic fresh-water fishes seldom are of any particular importance in showing terrestrial geographical relationships.

3. East Indian Archipelago

This term is used here to indicate the entire region from Sumatra and

the Philippines to and including Australia. Relationships within this archipelago inescapably involve Wallace's and Weber's Lines and these have been ably discussed by Mayr (1944). His fish data are mostly from de Beaufort (1913 and 1926) and are thus somewhat outdated. In addition he has misinterpreted some ichthyological facts and not realized the importance of others.

Makassar Strait forms the most spectacular zoögeographical boundary to be found among the world's fresh-water fish faunas. To the west lies Borneo, teeming with 17 families and 300 or more species of primary fresh-water fishes. Only 85 miles to the east lies Celebes, with two solitary species of primary fresh-water fishes,[3] both probably introduced by man. Celebes, like Borneo, has a few secondary forms (Cyprinodonts and a Synbranchid), as well as a peculiar small group of vicarious Atherinidae, but the difference from the magnificent Bornean fish fauna is very close to awe-inspiring. (See especially the volumes of Weber and de Beaufort.)

South of Makassar Strait, Wallace's Line is not quite so spectacular, since the primary fresh-water fish fauna of West Java is much smaller than that of Borneo, whilst that of East Java and Bali seems to be impoverished. Comparing Java as a whole with Lombok, Sumbawa and Flores, we find 12 families and nearly 100 species of primary fresh-water fishes immediately to the west of Wallace's Line (data mostly from Dammerman, 1929) and but four families and five species of primary fresh-water fishes to the east of it (de Beaufort, 1913). Of these five, at least three have probably been carried across by man as food fishes,[4] and it is notable that two of them are the same species that have crossed Makassar Strait into Celebes. The remaining two primary species which have crossed to the east of Lombok Strait are small fishes of two Cyprinid genera (*Rasbora* and *Puntius*) which perhaps have crossed sea barriers elsewhere.[5]

The Philippines deserve especial mention. (See Herre, 1924a, 1924b, 1928.) Bornean primary fresh-water fishes exist in Palawan and the Calamianes Islands, which are on the Bornean continental shelf and are, zoölogically, completely Bornean in affinity. One species (*Puntius*; called also *Barbodes* by Herre, and *Barbus* by others) has gotten from the Calamianes to Mindoro. The continental shelf appears to break down to some extent along the Sulu Archipelago, but three genera (including *Rasbora* and *Puntius* again) have gotten a foothold in Mindanao, coming up through the Sulu chain, and two or three races or poorly differentiated species of each genus occur in different parts of the island. In Lake Lanao, located in central Mindanao, *Puntius binotatus* (the same species which crossed Lombok Strait from Bali) has flowered into a most remarkable lake fish-fauna, several species of which are so peculiar as to have been placed in different genera (Herre, 1924a and b; 1933). I intend to take up the evolutionary problem of the Lanao fish fauna in another place. Finally, Mindanao possesses an endemic Clariid catfish, but some Clariids do enter brackish water, according to Weber and de Beaufort (1913) and Dammerman (1929).

All of the islands between the Sunda continental shelf and the Australian-New Guinean continental shelf, including all of the Philippines except Mindanao and the Palawan-Calamianes group, form an ichthyological no-man's-

[3] *Anabas testudineus* and *Ophicephalus striatus*. Both are commonly carried about alive by man as food fishes, the latter more than the former. *Anabas* is said occasionally to enter brackish water.

[4] The three are *Anabas testudineus*, *Ophicephalus striatus*, and *Clarias batrachus*. Both the first and the last are said occasionally to enter brackish water,

[5] Holly (1927) has recorded 11 species of primary fresh-water fishes from the ichthyologically little known island of Sumba (Sundalwood), southeast of Sumbawa and Lombok. The species are all found in Borneo, Banka, and Sumatra, and four of them (*Rasbora kalochroma*, *Ophicephalus melanosoma*, *O. bankanensis*, and *Betta anabatoides*) are unknown in Java. Some mistake in the locality must have occurred, and I suggest that Holly's whole collection came from somewhere in Borneo or Sumatra.

land, so far as primary fresh-water fishes go. Three common Sundaland species belonging to primary groups are widely spread over many of these islands—*Clarias batrachus, Ophicephalus striatus,* and *Anabas testudineus*—but all three are air-breathing foodfishes often carried about alive in the Orient, especially the *Ophicephalus,* and both of the other two are reported to enter brackish water. Two or three more *Clarias* also occur in the Philippines but some enter brackish water. Other primary fishes have entered this no-man's-land, apparently by non-human agency, only at Mindoro (1 species), and at Lombok (2 species). In both instances the same genus (*Puntius*) is concerned, in addition to *Rasbora* in Lombok. When one considers the 17 or 18 families and 400 or more species of primary fresh-water fishes of Sundaland, Wallace's Line (essentially the edge of the Asiatic continental shelf) stands out as a great major faunal boundary of excessive sharpness.

Perhaps the most interesting thing about it is that other Asiatic vertebrates, even amphibians, show no such strict limitation to the Sunda Shelf as do the primary fresh-water fishes (Mayr, 1944). These primary fishes are able to migrate slowly across any well-watered land. But only a very small number of species of any primary fresh-water fish fauna seems able to cross a salt-water barrier of any description. If Sundaland had been connected with the islands to the eastward at any time since the Eocene, primary fresh-water fishes of some type should swarm in the islands to the east of Wallace's Line. That they do so only in Mindanao proves to my entire satisfaction that there has been no land connection except with Mindanao, and that Mindanao is therefore probably part of Sundaland. Moreover, if it proves that, it also proves that other vertebrates, including amphibians, can and do cross sea barriers with relative ease, however they may do it.

Weber's Line, as Mayr (1944) shows, is a line of faunal balance. From the fresh-water fish evidence, the Australian-New Guinean continental shelf, including the Aru Islands but excluding Halmaheira, Ceram and Timor, is a more significant line. This shelf marks the westward limits of the Melanotaeniin fishes (Regan, 1914; Weber and de Beaufort, 1922), which are perhaps the most generally characteristic of Australian fresh-water fishes. Although the Melanotaeniins are only vicarious fresh-water forms, belonging to the primarily marine family Atherinidae, and are said by Regan (1914) not to be of much importance in terrestrial zoögeography, it is very suggestive to note their absence from Ceram and Halmaheira, where so many vicarious or diadromous Papuan species are to be found.

Australia and New Guinea possess only two species of primary fresh-water fishes, the Queensland Ceratodontid lungfish (*Neoceratodus*) and an Osteoglossid, *Scleropages leichardti,* common in Queensland and once recorded from New Guinea on the basis of a photograph.[6] Both are solitary relict forms, whose ancestors got to Australia previous to the Cenozoic, probably at about the time Marsupials entered that continent. The lungfish has no close living relative. The *Scleropages* has as its only close living relative another species (*S. formosus*) found from Siam and Indo-China to Borneo. Three other living Osteoglossid species exist in Africa and South America, but the family has a still wider Eocene distribution (Myers, 1938). That these ancient fishes, although considered primary fresh-water forms today, may have had close relatives capable of crossing sea barriers, is entirely possible. Indeed, it would seem probable that they did, for if Australia (and New Guinea) had been connected by a dry-land bridge with Asia during

[6] Mayr (1944) thus had no basis at all for stating that the absence of primary fresh-water fishes of Seran (Ceram) and Kei indicates that these islands have had no continental connection with New Guinea. Fowler (1941) recognized two Queensland species of *Scleropages,* but *S. guntheri* is a very doubtful species.

the Mesozoic, Australia should today be a veritable living museum of Mesozoic types of fresh-water fishes. That only two such species exist in a continent whose fresh-water fish fauna is notably depauperate, and in which there has, therefore, been less competition than elsewhere, points to the conclusion that neither Australia and New Guinea, nor any of the other islands east of the Sunda Shelf, have ever had wide open dry-land connection with Asia. This is directly in line with Simpson's conclusion (1940, pp. 156-157) that the mammal colonizers of Australia reached that continent from Asia by what he terms a "sweepstakes" or "island hopping" route across one or more sea barriers.

All the rest of the comparatively depauperate Australian-New Guinean fresh-water fauna is composed of secondary fresh-water fishes (such as *Synbranchus bengalensis*; see Regan, 1914), of vicarious representatives of marine groups such as Atherinidae, and of a few strange diadromous families such as the Galaxiids.

Except for the two relict primary species, Australia and New Guinea have no primary fresh-water fishes. Any paleogeographical conclusions to be gained from the rest of the fresh-water fish fauna is, therefore, open to question simply because of the presumption that most or all of the species either can or do enter the sea with impunity. Iredale and Whitley (1938) and, more recently, Whitley (1947), have delimited distinctive Australian fluvial regions based on fresh-water mollusks and fishes, but so far as the fishes are concerned, it would appear that these regions may be as much reflections of the marine faunal composition on the adjacent coasts as they are anything else. In any event, comparatively little is yet on record regarding the possible seagoing abilities of most of the Australian and Papuan vicarious fresh-water fishes.

4. New Zealand

New Zealand has no primary or even secondary fresh-water fishes and there is, therefore, nothing in the fish evidence upon which to base any positive opinion in regard to its former connection with Australia or any other land mass. However, that New Zealand does not have either primary or secondary true fresh-water fishes, as it should have if it has been connected to Australia or especially to South America (directly or via Antarctica) during the Cretaceous or early Cenozoic, indicates that any continental connection it may have had must have been rather far back in the Mesozoic.

That the Galaxiids indicate any connection is very doubtful, in spite of their peculiar distribution (South Africa, South Australia, New Caledonia, New Zealand, Southern South America). Regan (1906) pointed out that some forms, at least, are catadromous, and Scott (1941) shows that at least one Tasmanian species enters the sea. Hefford (quoted from Phillips, 1940) described the breeding of *Galaxias attenuatus*, which appears to have tide-controlled spawning habits similar in some ways to those of the California grunion, an Atherinid. That the young of some forms are found at sea is established, and it is probable that marine wandering is the key to the family's distribution.

5. Formosa and Japan

There has never been much question but that the main islands of Japan were connected with the mainland at no very distant time, geologically speaking, and the fishes demonstrate this. The large primary fresh-water fish fauna of Formosa is practically identical with that of adjacent Fukien

on the Chinese mainland, but not with that of Japan, and any apparently endemic species and genera should be accepted with caution until Fukien is more extensively fished. But Formosan relationship with the Luzon fauna, which appears in some terrestrial groups, is totally absent in the primary fresh-water fishes, simply because the Northern Philippines have not and apparently never have had a native primary fresh-water fish fauna. *Ophicephalus striatus, Anabas,* and *Clarias* are there, undoubtedly introduced by man, but nothing else except one or two secondary fishes. It may be that secondary or other fishes have gotten to Formosa from Luzon, by means of typhoon winds, but the fact that the species are also found on the mainland makes this difficult to determine. The Riu Kius have a very few fresh-water fishes, mostly Formosan species, and perhaps had a fairly recent but tenuous connection with that island.

6. Oceania

The islands of Oceania have not a single primary or secondary fresh-water fish except for recent introductions by man. The nearest thing to a native fresh-water fish anywhere is a Galaxiid on New Caledonia (Weber and de Beaufort, 1915; Scott, 1936), which could perhaps have gotten there by sea from Australia. If there had been any great continental land mass in the Pacific during any part of the Cenozoic it should have had primary or secondary fishes, or at least have evolved some recognizable, peculiar, vicarious fresh-water types. That no such types are evident on a single island of Oceania should of itself dispose of the notion of any such continental mass as J. W. Gregory (1930) postulated.

The fishes which occur in the fresh waters of the islands of Oceania are well illustrated by Weber and de Beaufort's list of New Caledonian fishes (1915). There are diadromous fishes such as *Anguilla,* some of the gobies, and the Mugilidae, and there are sporadic fresh-water fishes such as *Kuhlia, Ambassis, Lutianus* and some other gobies, but nothing more. Complementary fresh-water fishes, such as *Sicyopterus, Stiphodon,* and *Cestraeus,* are dominant.

7. The Galapagos

This is the only group of islands on the American side of the Pacific which are of a size and distance from the mainland sufficient to make their inclusion necessary. There is only a single fresh-water stream of consequence in the entire Archipelago. It is on Chatham Island (Watering Bay) and I have fished in it. It appears to contain but one species, *Agonostomus hancocki* (Seale, 1932), a diadromous, complementary fish related to American mainland forms and perhaps not specifically separable. Since Dr. Hubbs tells me he has gotten young *Agonostomus* in the sea at Acapulco, this fish has no direct bearing on the origin of the Galapagos fauna.

8. Sea Crossings by Primary Fresh-Water Fishes*

The few primary fresh-water fishes which are presumed to have crossed ocean barriers between Pacific islands by other than human agency are confined chiefly to three genera of Cyprinidae and to three points of crossing. One *Puntius* (an endemic species) exists in Mindoro; its ancestors certainly came via the Calamianes group. Three genera *(Puntius, Rasbora, Nematalestes)* have reached Mindanao from North Borneo, apparently via the Sulu chain. One *Puntius* and one *Rasbora* have reached Lombok and Sumbawa from Bali or

Java, but whether they have recognizably differentiated on the different islands has not been adequately ascertained.[7]

The Mindoro and Lombok crossings involve one and two species respectively. The species are small and common. The Lombok fishes may have been carried across by man, especially Chinese, who like to transport small live fishes, but I doubt it. The Mindoro species is endemic, is not found in the well-fished Calamianes Islands, and was not carried by man. There may be more than one species in poorly-fished Mindoro.

The Mindanao crossing is more complicated. *Puntius binotatus*, a widely distributed species in Sundaland and the same one that made the Lombok crossing, must have gotten across at least as far back as the early Quaternary, for from it evolved the recent but rich fauna of closely related forms in Lake Lanao (Herre, 1924a; 1933).[8] Two or three other races or species of *Puntius* are also found in Mindanao streams, but these are all close to or inseparable from *P. binotatus*. Two forms of *Nematabramis* are known from Mindanao (Herre, 1942a). They may not be really different and one at least is identical with a North Borneo species. The two Mindanao *Rasbora* are close to Bornean forms. Apparently *Rasbora, Puntius* and *Nematabramis* are found on several of the Sulu Islands, from Basilan to Tawitawi.

Various writers (see especially Matthew) have pointed out that smaller terrestrial animals undoubtedly have been transported across sea barriers on rafts of jungle vegetation which float out of tropical rivers during periods of flood. I have seen such rafts myself—even one supporting a ten-foot boa-constrictor! But fresh-water fishes do not cross seas on rafts.

Darlington (1938) has searchingly discussed this and other methods of over-water dispersal, especially by winds and storms. It is now perfectly well authenticated that waterspouts caused by tornadoes can and do occasionally pick up small fishes and deposit them at a distance (Gudger, 1929a, 1929b; Bajkov, 1949). Mindoro and the Calamianes are in the typhoon area, which could easily explain the single *Puntius* in Mindoro. Lombok and Sumbawa are not in a typhoon area. But waterspouts do occur in many places and they do pick up fishes and upon rare occasions carry them for short distances. The distances involved here are comparatively short. We do not know anything about the specific salt-tolerance of the two species concerned, but if they could not have navigated a short stretch of salt water and were not introduced into Lombok and Sumbawa by man, there are only two ways they might have crossed Lombok Strait—by waterspout or (as suggested by Mayr) upon a sheet of fresh surface water during heavy rains. Lombok Strait was evidently much narrower (and Lombok and Sumbawa were one island) during the Pleistocene. Crossing would have been easier under such conditions. In any event I do not think these two fishes present much of a problem.

Darlington (1948, pp. 7-8) has presumed that the Cyprinids had to cross sea barriers to reach both the Palawan-Calamianes group and Mindanao. I think this very unlikely for the former. Palawan and even Busuanga have too many species (not only of fishes) in common with North Borneo, and a land connection seems certain. Tentatively, I have previously agreed with Darlington that there was no recent dry land connection of Mindanao with Borneo, but this conclusion appears to be untenable upon careful study. The three genera which reached Mindanao still exist on the larger Sulu is-

[7] My student, Dr. Martin R. Brittan, has recently (1950) completed a revision of the genus *Rasbora* which notably clears up many points in systematics. The thesis has not as yet been published.

[8] At my request, the late Dr. Bailey Willis of Stanford made a special study of the evidence regarding the age of the lava flow which dammed up and formed Lake Lanao. He stated that the known rate at which lava is eroded by stream and waterfall action indicates an age of not over 10,000 years for the lava flow and the lake. I am preparing a paper in regard to the Lanao fish fauna.

lands, and it is wholly possible that faulting has recently deepened some of the inter-island channels, which are still all fairly shallow. The North Borneo fresh-water fish fauna is notably depauperate, compared to South Borneo, and a dry isthmian link along the Sulu chain in the Pleistocene would have freely allowed to cross just the fish which did.[9] It is, therefore, my opinion that the Mindanao fresh-water fishes arrived via a dry Sulu land bridge, and certainly not earlier than the Pliocene.

9. Conclusions

There is nothing in the distribution of the fresh-water fishes of the Pacific islands favorable either to continental drift or to J. W. Gregory's Pacific continent, and much that opposes the latter. In fact, the fish evidence points directly to the conclusion that the islands of Oceania are truly oceanic, in the sense of Wallace.

In the great Indo-Australian Archipelago the fish evidence very strongly supports the conclusion that there has been no dry land connection whatsoever between the islands of the Asiatic continental shelf (Sundaland) with Celebes or Lombok, or any of the islands to the eastward of these, during the entire Cenozoic. It also strongly indicates that Mindanao and the Palawan-Calamianes chain were connected by dry land with Sundaland during the Pleistocene, but that the other Philippines were never so connected during the entire Cenozoic. It further suggests that, even in the Mesozoic, there was never a dry land connection between Asia and Australia. Only three relicts of this Mesozoic fish fauna remain today—one Osteoglossid in Sundaland, another in Queensland (which has once been reported from New Guinea) and the Queensland lungfish.

The islands between Wallace's Line and the New Guinean-Australian continental shelf, and most of the Philippines (save the Palawan-Calamianes chain and Mindanao, which were part of Sundaland) are populated chiefly by fresh-water fishes of fairly recent marine origin, and which therefore give no indication of past land connections.

Most of the New Guinean-Australian fish fauna is of similar marine origin. Only the lungfish and the Osteoglossids are true fresh-water fishes, and fresh-water faunal districts in New Guinea and Australia based on fish distribution are based primarily upon fishes of close marine relationship.

There is nothing in the existing fresh-water fish faunas of New Zealand or any of the islands of Oceania east of the Philippines, New Guinea and Australia, to indicate any past continental connection.

That Japan and Formosa have only recently become separated from the mainland adjacent to each is plainly indicated by the fresh-water fishes. There is no possibility that Formosa and Luzon have been connected by continuous dry land during the greater part of the Cenozoic. Formosa has abundant native primary fresh-water fishes; Luzon has none.

There is no fresh-water fish evidence to indicate a continental connection of the Galapagos with the American or other mainland.

Finally, the evidence presented here and in my 1938 paper indicates strongly that primary fresh-water fishes, of all the major groups of vertebrates, are least capable of crossing sea barriers. The only other major vertebrate group so strictly limited by salt-water barriers are the burrowing caecilian amphibians, which are wholly tropical and very small in number. It follows that primary fresh-water fishes, above all other vertebrates, are the best indicators of the existence of sea barriers of long standing.

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[9] **Caecilians are amphibians which, unlike frogs, never appear to cross sea barriers. Caecilians are found not only in Basilan but also on Mindanao (specimen in Stanford collection).**

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TWO NEW AGONID FISHES FROM THE SEA OF JAPAN

By Harry Wyman Freeman

In the course of a general revisional study of the marine mail-cheeked fishes of the family Agonidae, now virtually completed, the two apparently unrecognized species herewith described were discovered. As the publication of the main study may be delayed it seems best to present these new species at the present time. Both are from the collection obtained in Japan in 1928 by Dr. Carl L. Hubbs (now of the Scripps Institution of Oceanography, La Jolla, California) for the University of Michigan. In 1930, the agonids of this collection were worked over at Michigan by Dr. Katsuzo Kuronuma, then a student of Dr. Hubbs. Unfortunately Dr. Kuronuma's manuscript was destroyed during the recent war; one of the new species is named for him. The other is named for Dr. Clark Hubbs (son of Dr. Carl L. Hubbs), who helped me while a fellow student in Professor Myers' laboratory at Stanford. In the specimen lists, UMMZ = University of Michigan Museum of Zoology, and SU = Natural History Museum of Stanford University.

Tilesina hubbsi, new species
Figure 1

Diagnosis: This species is distinguished from *T. gibbosa* Schmidt (1903, p. 16; 1904, p. 134, pl. 4), the only other known member of this genus, by the presence of 2 spines on the suborbital stay; of one sharp spine on the ventral rim of the orbit; and of a spine on the preorbital. There are 5 sharp spines or crests on the temporal ridge of this new species not present in *gibbosa*; the occipital crests are more prominent. The supraocular crests of the new species are greatly serrated and bear several spines on the posterior margins. The dorsad spine of the preopercle is more prominent and more elevated, and has a short blunt spine at its anterior base.

Description: Caudal peduncle short and slightly depressed, its depth 53.7 in standard length, its length 5.1. Body widest in pectoral region; width at pectoral base 10.7.

Head long, tapering anteriorly, 4.7 in length. Mouth moderate, lower jaw extending posteriorly to a vertical beyond middle of eye. No barbels on lower lip. Maxillary not reaching anterior rim of orbit, maxillary flap short and flat. Premaxillary large, expanded posteriorly. Snout elongated, 3.6 in head. One pair of spines on posterior part of nasal bones, directed posteriorly and slightly laterally. A short broad groove between nasals; nasals not fused anteriorly. A short anterior nasal flap, just lateral to nasal spine. Posterior nasal opening inconspicuous. A number of short plates with sharp spines anterior to eye. Preorbital spine present. Suborbital stay prominent, ending in one large and one small spine. Cheek below suborbital naked (without spines or plates). Preopercle with one flat, ventrally directed spine, and one sharp elevated spine which bears in front of it a short blunt spine. Opercle with a very low crest. Temporal ridge prominent with 5 sharp spines or crests. Eye moderate, orbit 5.3 in head; eye almost circular. Supraocular crests prominent, greatly serrated, with several sharp spines on posterior borders. Occipital region raised, with 2 blunt crests. Many small plates with spines in midline anterior to first dorsal becoming very numerous in occipital, temporal, and opercular regions. Interorbital slightly concave; width greater than half

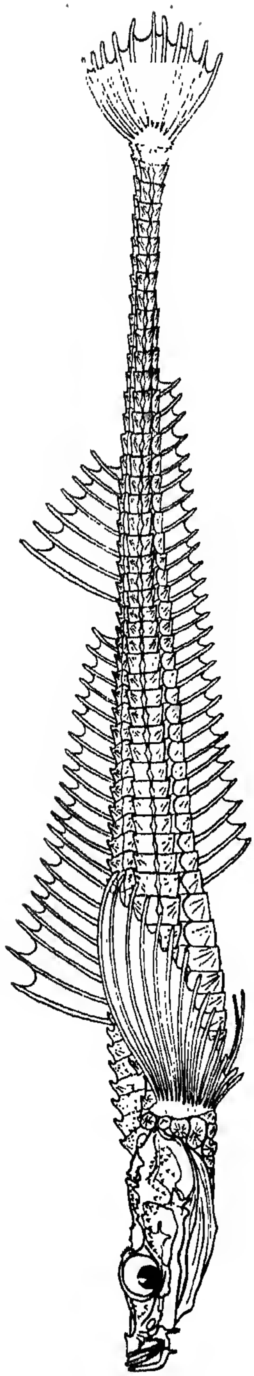

FIG. 1. *Tilesina hubbsi* Freeman. Holotype, UMMZ 158503. Standard length 204 mm. (Drawn by Judith Mottram.)

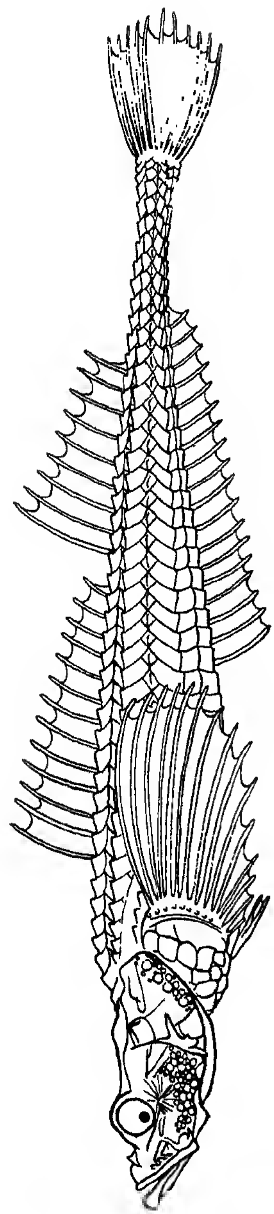

FIG. 2. *Occa kuronumai* Freeman. Holotype, UMMZ 160733. Standard length 157 mm. (Drawn by Judith Mottram.)

diameter of eye. Interorbital space 9.8 in head. Gular region and gill membranes without barbels. A few small, inconspicuous teeth on vomer and palatines.

Breast covered with heavy overlapping plates; each with a sharp, low, posteriorly directed spine.

One small pair and one large pair of plates anterior to pelvics. Several large plates with prominent spines anterior to pectorals. A row of plates with sharp, posteriorly directed spines on mid-ventral line between anus and anal, not, however, running forward to anus. Three plates with sharp spines anterior to anus between pelvics. No plates between ventro-lateral and ventral rows beneath pectorals. Plates of dorsal row become fused posterior to second dorsal fin; the spines, however, remain paired. Ventral plates of caudal peduncle paired except for posteriormost 2 plates, which are fused but whose spines remain paired. Lateral line takes over and occupies space on the anterior 4 plates of the dorso-lateral series. Ventrolateral series pass dorsally above pectorals. Anus lies between pelvics but is not very far advanced. Pectorals large but not extending to or past the middle of first dorsal as they do in *T. gibbosa*. Median fins not very high. Interdorsal 4.0 in distance from first dorsal to tip of snout. Anal inserted far anterior to second dorsal. All body plates bear sharp spines. A row of small spines between dorsal and dorso-lateral series in anterior half of body.

Fin and scale formulae: D. XXI, 7; A. 27: p. 15; plates in D. row 54; Ll. 55; plates between first A. ray and base of ventrals 10; plates between last A. ray and base of caudal 12; first dorsal inserted on plate 8.

Color in spirits: dorsal half of body dark chocolate brown, spotted with small black dots; ventral surface lighter brown, except caudal peduncle darker and spotted posteriorly. A blackish band from anterior end of snout through middle of eye across opercle to dorsal surface of pectorals, where it is continuous with the dark lateral line. Lateral line becomes paler caudad. Dorsal and pectoral fins with several series of black spots in vertical rows. A dark spot at free end of membranes supporting each anal ray. Pelvics pale.

I have seen but one specimen, the 204-mm. holotype, UMMZ 158503, from U.S.S.R.: Siberia, Sea of Japan, about 58°(?)N., from Toyama-ken Fisheries Experiment Station.

This species is named in honor of my friend and fellow student, Dr. Clark Hubbs, now of the Department of Zoology, University of Texas, Austin, Texas.

Occa (Iburina) kuronumai, new species
Figure 2

Diagnosis: No body plates possess sharp spines. This species is distinguished from other members of the subgenus by the presence of many thick plates of moderate size beneath the suborbital crest, and of several large plates on top of head in midline just anterior to the occipital crest. Cheek behind eye covered with many large thick plates. Many plates of moderate size cover the body between anterior ventral and anterior ventrolateral series beneath pectorals. This is an especially important character.

Description: Caudal peduncle short and stout, rectangular in cross-section at the posterior end; its depth 36.9 (35.2-38.9) in standard length, its length 5.8 (5.5-6.1). Body greatly broadened anteriorly; width at pectoral base 6.2 (5.6-6.9).

Head broad, its length 4.2 (4.1-4.3) in length. Mouth moderate, with lower jaw projecting and extending to posterior rim of orbit. Maxillary

extends to a vertical between middle of eye and anterior rim of orbit; one short flap on posterior maxillary. Premaxillary large, expanded posteriorly. Snout broad and short, 4.6 (4.4-4.7) in head. Nasals short. Nasal spine blunt, covered with many short spines. No barbels on snout, lower jaw, or branchiostegal membranes. Anterior nasal flap large, just laterad of the nasal projection. Posterior nasal flap very small, just anterior to eye. Cheek below suborbital crest with many thick plates of moderate size. Suborbital stay not spiny. Entire rim of orbit serrated. Supraorbital crest low. Preopercle with one sharp posteriorly directed spine and 2 flat blunt spines beneath. Opercle with a low crest. Opercular flap with many large plates. Temporal crest broad and not spiny. Occipital crest low but not spinous. Eye moderate, 5.0 (4.7-5.3) in head. Cheek posterior to orbit with many large plates. Interorbital space broad, 4.4 (4.2-4.6) in head. Median dorsal plates anterior to first dorsal spine very small and prickly. Gular region covered with heavy plates of moderate size; smaller plates under gill membranes.

Breast with large non-spinous plates interspaced with more numerous smaller plates. Two to 3 pairs of plates anterior to pelvics. The region between pelvic base and first anal ray with many small and moderate sized strong plates. Body eight-angled in region of first dorsal, six-angled at caudal peduncle becoming rectangular posteriorly. Lateral line takes over and occupies space on anterior 4 or 5 plates of dorso-lateral series. Ventro-lateral series of plates runs anteriorly to dorsad edge of pectoral. Space between ventro-lateral and ventral series beneath pectorals covered with many plates of moderate size. Anus situated far forward between pelvics. Pectorals moderate, extending to about midpoint of first dorsal. Distal border of pectorals not emarginate. Pelvics short. First dorsal inserted on eighth plate of dorsal series. Interdorsal 4.9 (4.8-5.0) in distance from first dorsal to tip of snout. Dorso-lateral series of plates converge 7 to 8 plates posterior to the second dorsal.

Fin and scale formulae: D. XII, 9 (X-XII, 9-10); A. 19 (18-19); P. 16 (16-16); plates in D. row 41 (40-42); Ll. 43 (42-44); plates between first A. ray and base of ventrals 13 (11-14); plates between last A. ray and base of caudal 9 (8-9); first dorsal inserted on plate 3 (2-4).

Color in spirits: dorsal half of body and head dark grey to black; beige on ventral surface except for caudal peduncle which is dark grey posteriorly. Dorsal fins, caudal, and pectorals blackish, with several series of darker spots in vertical rows on rays or in membrane between rays. Pelvic fins beige. Anterior half of anal fin pale, posterior half light grey.

Relationships: This new species is obviously a member of the *Occa* group. It seems to be most closely related to *O. iburia* Jordan and Starks (1905, p. 585) and *O. kasawae* Jordan and Hubbs (1925, p. 291, pl. 11, fig. 1) as they have in common the following: snout short, flattened, and quite broad; 12 to 15 spines in first dorsal; pectorals with 16 to 19 rays; plates of dorsal series 41 to 43; 43 to 45 plates in lateral line; plates present between anterior ventro-lateral series beneath pectorals. For these reasons I have placed it in *Iburina*, which I consider to be a subgenus of *Occa*.

I have examined 5 specimens from the following localities: 4 from Sea of Japan, close to Niigata, from Niigata market, C. L. Hubbs and K. Sakamoto, (UMMZ 160733, holotype, 157 mm.; 158488, paratype, 151.5 mm.; 158489, paratype, 163.5 mm.; SU 16724, paratype, 155 mm.); one from Sea of Japan, Niigata-ken Fisheries Experiment Station, (UMMZ 158486, paratype, 137 mm.). Known only from these specimens.

This species is named in honor of Dr. Katsuzo Kuronuma who set it aside as a new species in 1930 while working as a graduate student at the University of Michigan, but whose manuscript, unfortunately, was destroyed by fire in World War II.

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SOME FORGOTTEN BUT AVAILABLE NAMES FOR INDIAN FISHES.—In the "Supplement to the Fishes of India" (London, 1888; pp. 779-816) Sir Francis Day published some fish names which appear to have been completely forgotten. These names were used by Col. Tickell in an unpublished manuscript on Tenasserim fishes utilized by Day, and a few of them were formally proposed by Day as new genera and species (e.g., *Acanthonotus* and the specific name of *Leiocassis fluviatilis*). Others were not accepted by Day, but were quoted by him in synonymy in connection with a description. They are therefore validly published and available for use if Day's identifications prove to be wrong, if preoccupation makes older names unusable, or if generic, specific, or subspecific splitting occur. None of these names appears ever to have found its way into the Zoölogical Record or the various generic nomenclators. The forgotten names are:

Acanthurus tristis Tickell (Day), p. 788. Type locality Arrakan. Placed by Day in the synonymy of *A. tennentii*, but perhaps a good form.

Malacocanthus Tickell (Day), p. 791. Type hereby designated as *M. coccinicauda* Tickell (Day). Apparently a synonym of *Pseudochromis*, but perhaps available for a subgenus.

Malacocanthus coccinicauda Tickell (Day), p. 791. Type locality Saddle Island, off Kyouk Phoo. Placed by Day under *Pseudochromis fuscus* but perhaps a good species or subspecies.

Malacocanthus bicolor Tickell (Day), p. 791. Type locality same as preceding form. Placed by Day under *Pseudochromis fuscus* but perhaps a good species or subspecies.

Geneiates Tickell (Day), p. 804. Type by monotypy and/or present designation *G. ferruginosus* Tickell (Day). Probably a synonym of *Brotula* but perhaps a good genus. Hubbs (Copeia, 1944: 163) has mentioned this name in his discussion of *Brotula*.

Geneiates ferruginosus Tickell (Day), p. 804. Type locality Saddle Island, off Kyouk Phoo, Arrakan. Doubtfully identified by Day with *Brotula multibarbata* from Japan. See also Hubbs (loc. cit.).

Duxordia Tickell (Day), p. 805. Type by monotypy *Duxordia fluviatilis* Tickell (Day). Probably a synonym of *Leiocassis* but perhaps available for a subgenus. Day described the type species as a new species, *Leiocassis fluviatilis*, on p. 805. The type locality is the Anin, a stream arising near Weywoon, Wagroo, Tenasserim.

The fact that "manuscript names" mentioned without acceptance but in connection with a description are validly published and available for use should restrain authors from mentioning them.—George S. Myers.

PHYSICULUS JORDANI, A NEW GADOID FISH FROM DEEP WATER OFF JAPAN[1]

By James Böhlke and Giles W. Mead

Among those fishes labeled *Physiculus japonicus* Hilgendorf in the Stanford University collections we have found a single specimen apparently different from the others. After comparing this fish with the species and synonyms listed by Norman (1937, p. 54) and with other related forms referred to in the Zoölogical Record, it is evident that this specimen represents an undescribed species. In many characters, notably by the absence of the chin barbel, the new species seems to be most closely related to *Physiculus edelmanni* Brauer 1906, from deep water off the coast of East Africa, and *P. filifer* (Garman) 1899, from off the Pacific Coast of Panama.

Physiculus jordani, new species

Holotype: SU 21759; collected by the U.S. Fish Commission Steamer "Albatross", May 4, 1900, off Tsurugi Saki Light (S. 80° W. 4.3 m.), Honshu Island, Japan, Station 3695; depth 259-110 fms.; collected with an eight foot Tanner beam trawl. This specimen was acquired by exchange from the United States National Museum many years ago as *Physiculus japonicus*.

Description: Measurements of holotype[2]: Standard length 162, total length 182, greatest width of body 19 (12), greatest depth of body 27 (17), depth at ventral fin insertion 29 (18), least depth of caudal peduncle 3.5 (2), least width of caudal peduncle 1, length of caudal peduncle 15 (9), greatest width of head 26 (16), postorbital length of head 21 (13), fleshy interorbital 15.5 (10), snout 13 (8), eye 7.5 (5), maxillary 19 (12); tip of snout to first dorsal origin 40 (25), to second dorsal origin 49.5 (31), to anal origin 56.5 (35), to pectoral base 44.5 (27), to ventral origin 43.5 (27); length of base of first dorsal 7.5 (5), of second dorsal 102 (63), of anal fin 108 (67); pectoral fin length 24 (15), ventral fin length 24.5 (15), length of median caudal rays 10 (6), longest gill raker 4 (2).

First dorsal 8; second dorsal about 71; anal about 75; pectorals 22, 22; ventrals 6, 6; caudal 8-17-8 (possibly 7-19-7); gill rakers 5 + 10; branchiostegals 7.

General body form similar to *P. edelmanni* as figured by Brauer (1906, pl. 12, fig. 6). Greatest body depth 6 in standard length, 1.5 in head length. Body tapering evenly from anus to the very shallow peduncle; depth of caudal peduncle is contained 11.4 times in head; length of caudal peduncle (to base of median caudal rays) 2.7 in head. Head moderate, 4.1 in standard length. Snout short and broadly rounded, 3.1 in head. Eye small, 1.7 in snout, 2.1 in interorbital, 5.3 in head. Interorbital broad, flat or slightly convex, its width 2.6 in head. Maxillary 2.1 in head, reaching nearly to a vertical with posterior margin of pupil. Minute villiform teeth in bands on maxillaries and mandibles, absent from vomer and palatines. Branchiostegal membranes broadly united; joined to isthmus anteriorly; width of free fold about 2/3 diameter of eye. Gillrakers moderate, length of longest raker 10 in head.

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[1] Family Moridae, following the latest revision of the cods by Svetovidov, A. N., 1948, Gadiformes, *in:* Fauna SSSR, vol. 9, no. 4 (Zool. Inst. Akad. SSSR, new series, no. 34), 221 pp., pls. 1-72.

[2] These consist of measurements in millimeters followed, in parentheses, by the proportion in hundredths of the standard length.

Origin of the first dorsal fin above upper end of pectoral base, its distance from tip of snout 4.1 in standard length. Second dorsal distinct from first, distance from its origin to tip of snout 3.3 in standard length. Distance from snout to insertion of anal 2.9 in standard length. Ventrals inserted anterior to pectorals; their longest rays 1.6 in head length. Length of pectoral fin contained 1.7 in head. Midcaudal rays longest, their lengths about 4 in head. Chin barbel absent.

Peritoneum silvery inside, but in places so filled with black specks as to appear black.

Key to the Species of *Physiculus* Lacking the Barbel

1a. Ventrals 5, equal to or shorter than head; eye 4.8 in head; eye 1.15 in snout; anal with 66 rays............................*edelmanni* Brauer
2a. Ventrals 7, much longer than head; eye 4 in head; eye 1.3 in snout; anal with 70-71 rays.................................*filifer* (Garman)
3a. Ventrals 6, shorter than head; eye 5.3 in head; eye 1.7 in snout; anal with 75 rays.....................................*jordani*, new species

Relationships: *Physiculus jordani* may be separated from *P. edelmanni* Brauer (1906, p. 274, pl. 12, fig. 6) by the characters utilized in the key above. From *P. filifer* (Garman, 1899, p. 182, pl. 41, figs. 2 and 2a), in addition to the characters enumerated in the key, it differs in lacking the elongate rays of the first dorsal fin, and in the possession of much shorter pectorals (pectorals 1.7 in head for *P. jordani*, less than 1.0 in head for *P. filifer*).

Of the species of *Physiculus* with the chin barbel, *P. jordani* appears to be closest to *P. argyropastus* Alcock (1893, p. 180, pl. 9, fig. 2), *P. grinnelli* Jordan and Jordan (1922, p. 22, pl. 1, fig. 3), and *P. nigrescens* Smith and Radcliffe (in Radcliffe, 1912, p. 105, pl. 22 fig. 1). The last three may be separated from each other on the basis of the fin ray counts, as follows:

	Second dorsal count	Anal count
P. grinnelli	73	65
P. nigrescens	66	72
P. argyropastus	55	57

Thus, *Physiculus jordani* is immediately differentiated from *P. grinnelli* and *P. argyropastus* by the number of fin rays, approaching only *P. nigrescens* in this respect. In addition to the differences in fin ray counts, *P. jordani* can be distinguished from *P. nigrescens* by its smaller eye, wider interorbital space, and gill raker count.

Named for David Starr Jordan.

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A NEW CUSK-EEL OF THE GENUS OPHIDION FROM CALIFORNIA WITH NOTES ON THE GENUS

By Robert R. Harry

While the writer was preparing a review of the Pacific cusk-eels of the genus *Otophidium*, two remarkable, though immature, specimens of the genus *Ophidion* from Santa Catalina Island off California were referred to him by the Bureau of Marine Fisheries, California Division of Fish and Game. These specimens have 7-8 gillrakers on the first arch, while all other known species of the genus *Ophidion* apparently have only 4. This new species is referable to the genus *Ophidion* because it (1) lacks opercular and ethmoid spines, (2) lacks pyloric caeca, (3) lacks scales on the head, (4) has a simple flat supramaxillary on the outer face of the maxillary, (5) has non-imbricate scales on the body arranged in oblique series. Apparently only two other species of *Ophidion (nigricaudum* and *iris)* are recorded from the Pacific Ocean, and these are known from single localities off Mexico.

Tentative Key to the Pacific Species of the Genus Ophidion

1a. Four erectile gillrakers on the lower limb of first arch; head length 4.9-5.1 into standard length.
  2a. Teeth in roof of mouth larger than those in jaws; a prominent dark caudal spot (San Refugio Bay, Mexico)............................... ....*Ophidion nigricaudum* Breder (1936, p. 44)
  2b. Teeth in roof of mouth not larger than those in jaws; no dark caudal spot (Gonzago Bay, Mexico)..........*Ophidion iris* Breder (1936, p. 44)
1b. Seven or eight erectile gillrakers on lower limb of first arch; head length 7.6-7.9 into standard length (Santa Catalina Island, California) ....*Ophidion novaculum*, new species

Ophidion novaculum, new species
Figures 1 and 2

Holotype: Stanford University 15964; 82.5 mm. in standard length; collected by Fred Woodworth on the research vessel "Yellowfin", at the surface under a light; depth of water 18 fathoms; time 8 P. M. on January 15, 1950, at Avalon Bay, Santa Catalina Island, southern California.

Paratype: SU 15965; 84 mm. in standard length; collection data as for holotype.

Description: In the following description the measurements and counts for the holotype are given first and are followed (in parentheses) by those for the paratype. Measurements were made to the nearest tenth of a millimeter and divided into standard or head length as indicated. Both types appear to be very similar and the characteristics described agree in both specimens.

Body elongate, strongly compressed, deepest near dorsal origin; greatest depth 11.0 (10.2) into standard length.

Head small, strongly compressed, not so deep as body, its length 7.9 (7.6) into standard length. Head width distinctly greater than body width. Snout short, with lateral and indented medial ridges above the nostrils; snout length 3.9 (4.0) into head length. Nostrils in a line between middle of eye and tip of snout; anterior nostril a transverse slit, without a

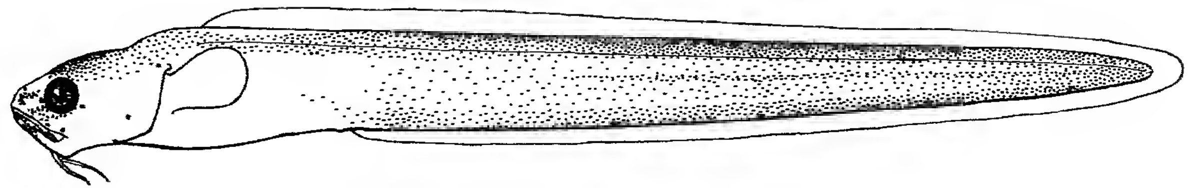

FIG. 1. Holotype of *Ophidion novaculum.*

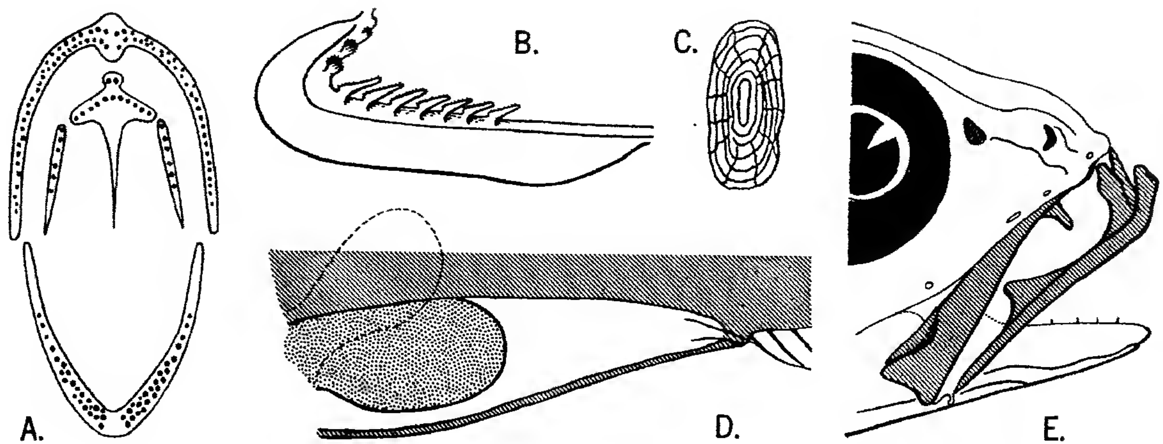

FIG. 2. Paratype of *Ophidion novaculum.* A. Dentition of upper and lower jaws. B. First right gill arch. C. Scale from behind tip of pectoral fin. D. Semidiagrammatic representation of left side of body cavity and air bladder. E. Side of head with upper jaw protracted.

raised rim; anterior nostril not under a labial fold; posterior nostril larger, oval, without a raised rim, very near border of eye. Edge of prefrontal not modified into a spine; therefore, no spine inside posterior nostril. Eye round, its posterior border far before middle of head length; eye diameter 3.8 (3.3) into head length. Interorbital slightly convex, with 2 longitudinal ridges and a median depression. Mouth strongly oblique. Upper jaw slightly indented at symphysis. Maxillary extending almost to a vertical from posterior border of lens. Hindborder of maxillary indented (Fig. 2e). Length of upper jaw (from tip of snout to posterior end of maxillary) 2.3 (2.4) into head length. Lips not papillose. Lower lip viewed laterally distinctly included. Teeth (examined by staining with alizarin red S) in upper jaw minute, fixed, subequal, in 2-3 irregular series (Fig. 2a). Teeth in lower jaw fixed, confined to anterior part of mandible, in 2 irregular series, slightly larger than teeth in upper jaw. Vomerine teeth tiny, blunt, arranged in a wedge-shaped patch of a single row in width; wedge preceded anteriorly by 1-2 teeth. A single row of 6 teeth on each palatine. Gill membranes joined to isthmus behind pelvic fin base below a vertical from posterior border of eye. Gillrakers on first arch 3+7 (3+8). All the rakers on the lower limb are moderately long and slender with finely denticulated inner margins (Fig. 2b). Length of longest raker on lower limb slightly less than lens diameter; each raker erectile, and reaching almost to tip of next anterior raker. Rakers above angle very short, spinulate tubercles. Opercle ending behind in a weak membranous flap; no spines developed. Branchiostegal rays 9 or 10.

Scales minute, cycloid, elongate (Fig. 2c); width of each scale approximately one-half the length. The focus is generally in the center and the radii are very weakly developed. Head, belly, and predorsal region scaleless. Scales on remainder of body widely spaced, imbedded, not imbricate, irregularly arranged, at oblique angles to one another. Lateral-line indistinct, interrupted, extending to base of caudal fin.

Swim bladder large, simple, ovate, its wall very thin and transparent, without a foramen (Fig. 2d). Swim bladder terminating more than the length of the pectoral fin before the anus. Anteriorly the air bladder is not thickened. No air sacs imbedded above the anal fin. The lack of a posterior foramen in both types might indicate that they are females, but sexual dimorphism in the form of the air bladder is probably not developed by this stage. In all genera and species of the Ophidiidae of which I have examined adults (including the genera *Ophidion*, *Otophidium*, *Lepophidium* and *Genypterus*) there is sexual dimorphism in the form of the air bladder. The males have a posterior foramen covered by a thin membrane, but this peculiarity is lacking in the females. An explanation for this phenomenon apparently has not been found.

Pyloric caeca absent. Peritoneum not silvery or black; completely lacking pigment.

Dorsal fin origin before a vertical from middle of pectoral fin. Distance from tip of snout to dorsal origin 6.2 (6.3) into standard length. Anal fin origin distinctly more than the length of the pectoral fin behind the tip of this fin. Distance from tip of snout to origin of anal fin 3.4 (3.4) into standard length. Pectoral fin rays 24 (24) on the left side, 25 (24) on the right. Each pelvic fin with one articulated ray divided at the base; its origin under front of eye; longest branch not reaching a vertical from pectoral fin base.

Measurements in percent of standard length: Body depth 9.1 (9.8); head length 12.7 (13.2); snout length 3.3 (3.3); eye diameter 3.4 (3.1); interorbital width 2.8 (3.3); upper jaw length 5.5 (5.5); distance from tip of snout to dorsal origin 16.1 (15.8); distance from tip of snout to anal origin 29.6 (29.7); pectoral fin length 7.0 (6.0); oblique distance between tip of pectoral fin and anal fin origin 9.6 (10.6).

Coloration: Color pattern very distinct and well preserved. Both type specimens with same coloration. Head heavily pigmented on occiput and gular region; scattered melanophores on jaws, preorbital, snout, suboculars, gular region and branchiostegal membranes. Iris solid black. Body dusky with large scattered melanophores indistinctly arranged on the sides into two longitudinal bands and a suffuse median lateral stripe (in this respect somewhat like *Otophidium marginatum*). No blotches or vertical bands. All fins completely without pigmentation.

Relationships: *Ophidion novaculum* seems to be more specialized than any other form of the genus. It transcends the known limits of the genus in the high number of gillrakers, but it should be pointed out that in both *Lepophidium* and *Otophidium* there is one group of species with 4 erectile rakers on the lower limb of the first arch and another group with 7 or more. This brings up the question of whether *Ophidion novaculum* might be the young of one of the species of *Otophidium* with a high number of gill-rakers. This subgroup of *Otophidium* is known only from the temperate eastern Pacific and *Ophidion novaculum* occurs within this range. The fact remains that the only consistent difference found between the closely related genera *Ophidion* and *Otophidium* is the presence of a strong opercular spine in the latter genus and its complete absence in the former. Thus the opercular spine might not be developed in the small types of *Ophidion novaculum* and this species would actually be the young of an *Otophidium*. Nevertheless, I have examined young specimens of all the known eastern Pacific species of *Otophidium* down to those less than one-half the length of the types of *Ophidion novaculum* and they all have very well-developed opercular spines. In fact, in many instances the spines are proportionately larger in the young than in the adults. The largest specimen of *Otophidium* examined that lacked the opercular spine was a postlarva, 37 mm. in standard length. The smallest specimen of *Otophidium* found that possessed an opercular spine was a juvenile, also 37 mm. in standard length. The opercular bones of the paratype of *Ophidion nbvaculum* were stained with alizarin red S and the flesh dissected away on one side. There is no trace of a spine on the preoperculum (as has been reported for *Dannevigia* Whitley, a genus related to *Lepophidium*) nor on the operculum. The posterior border of the operculum is rounded as in the Atlantic species of *Ophidion* examined (including the generic type, *Ophidion barbatum* Linnaeus).

The types of *Ophidion novaculum* were compared with specimens of *Otophidium taylori* down to 72 mm. in length and found to be quite similar in practically all body proportions, and somewhat similar in coloration. Some of the prominent differences between *Otophidium taylori* and *Ophidion novaculum*, based on individuals of the same size (72-88 mm. in standard length), are: (1) a prominent opercular spine present in *taylori* but completely lacking in *novaculum*; (2) teeth on vomer irregularly arranged in at least 2 rows and in a triangular or wedge-shaped patch versus regularly arranged in a single wedge-shaped row preceded by 1-2 teeth; (3) approximately 15 teeth on the palatine arranged anteriorly in 3 rows versus approximately 5-6 teeth arranged in a single row; (4) teeth in upper jaw anteriorly in 3-4 rows versus 2 rows; (5) teeth in lower jaw in 4-5 rows versus 2-3 rows; (6) in general the teeth on the jaws, vomer, and palatines are twice as large in *taylori* as those in *novaculum;* (7) pharyngobranchial teeth in large patches of approximately 10 or more teeth in width versus small patches of only a few teeth in width; (8) pseudobranchiae consisting of 6-7 tufts versus 4; (9) eye larger in *taylori* (1.3-1.5 times) than in *novaculum;* (10) posterior nostril of *taylori* one-half the size of this structure in *novaculum;* (11) anterior nostril round with a raised tube versus crescent-shaped without a tube. In specimens of nearly the same size or larger than the types of *novaculum* (1) roof of mouth heavily pigmented versus completely lacking pigmentation; (2) peritoneum on belly and lower sides dusky or

dark versus complete lack of pigmentation; (3) dorsal and anal fins edged in brown or black versus complete lack of pigmentation in *novaculum*.

From the literature *Ophidion novaculum* superficially appears to be closest to the rare *Ophidion graellsi* (Poey, 1861) from the Atlantic. *Ophidion novaculum* agrees with *O. graellsi* in having 7-8 gillrakers on the lower limb of the first arch. Fortunately the specimen of *graellsi* described by Jordan and Evermann (1898, p. 2488) from Havana, Cuba (SU 1920; originally received from Poey), has been available for study. This specimen is not an *Ophidion* but shows closer relationships to the genera *Lepophidium* and *Genypterus*. It disagrees in several significant characters with the type of *O. graellsi*, but these differences might be attributed to the great difference in size between the specimens. In any event, the original description of *O. graellsi* by Poey (1861, p. 425) clearly indicates that he is also describing a species close to or in *Lepophidium*, and that this form should be removed from the genus *Ophidion*. The status of *O. graellsi* and several other unusual forms in this family will be discussed in a subsequent paper.

As has been previously intimated, *Ophidion novaculum* probably represents an offshoot well separated from all other members of this genus. This opinion is based primarily on the high number of gillrakers in the new species. In most other characters *O. novaculum* shows close agreement to other members of the genus. A few of the most striking differences between *O. novaculum* and the other Pacific species of the genus are listed, but (3) to (5) might be due to stage of development: (1) gillrakers 7-8 on the lower limb of the first arch in *novaculum*, as compared to 4 in *nigricaudum* and *iris*; (2) maxillary extending to a vertical under lens instead of at least to midway between posterior margin of pupil and eye; (3) predorsal region and belly scaleless versus scaled; (4) pelvic fins shorter, not reaching a vertical from pectoral fins, rather than extending well beyond the pectoral base; (5) vertical fins unpigmented instead of irregularly edged with dark.

The types of *Ophidion novaculum* are young but in all other species of ophidiids I have examined, the adult characters (except coloration) are well developed by this stage, and there should be no trouble in identifying adults with these specimens. The coloration will perhaps be different in larger examples, but this character is so variable, even among individuals of the same species in *Ophidion*, that it would be only of secondary use in identifications.

It is very possible that future collections will uncover additional species of *Ophidion* with a high number of gillrakers related to *O. novaculum*. In such event it might be advisable to erect two subgenera on the basis of gillrakers, but this step does not seem worth while at the present time. These species are most likely to be found in the central eastern Pacific, which on the basis of our present knowledge, is the center of distribution of the family.

Acknowledgments: I wish to thank Miss Anita Daugherty, Mr. Fred Woodworth, Mr. John Radovich, and Mr. John Fitch, all of the California Division of Fish and Game, for making these specimens available, and Dr. Carl L. Hubbs of the Scripps Institution of Oceanography and Dr. W. I. Follett of the California Academy of Sciences for reading the manuscript.

This new species is named *novaculum* (Latin = a dagger) because of the similarity of its body outline to a two-edged knife.

Notes on the Genus Ophidion: The Pacific species *Ophidion iris* and *O. nigricaudum* are poorly differentiated (see key in Breder, 1936, p. 47). Within most of the well known species of ophidiids studied by me there is individual variation from specimens having an iris uniformly black to those with the iris black above and silvery below. In addition, the caudal spot of *nigricaudum* could easily be an individual variation. The last key character given by Breder (see first key character of 2a and 2b, p. 1 of this paper) is of use, since there is sometimes specific variation in size of

teeth. Unfortunately most of the important characteristics for distinguishing cusk-eels are not mentioned for these two specimens.

The following species appear to belong in the genus *Ophidion: O. barbatum* Linnaeus (generic type) and *O. broussonetti* (Müller) from the Mediterranean, *O. beani* Jordan and Gilbert from the Gulf of Mexico, *O. nigricaudum* Breder and *O. iris* Breder from the Pacific coast of Mexico, and *O. novaculum*, new species, from California. The other species previously placed in *Ophidion* apparently should be referred to other genera. A surprisingly large number of the species described in the Ophidiidae have been placed in the wrong genus; and the genera of the family, particularly *Lepophidium*, are in need of revision.

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NEWS NOTES ON THE STANFORD CENTER OF FISH AND FISHERY WORK.—Nothing has previously appeared in this Bulletin regarding the staff and students working in ichthyology at Stanford, and it is felt that readers may be interested in our organization and personnel.

The Stanford Department of Biology has three administrative divisions: General Biology, located in Jordan Hall on the main University Quadrangle; the Natural History Museum, located in the Stanford Museum Building, about ¼ mile north of the Quad; and the Hopkins Marine Station, located on Monterey Bay, at Pacific Grove, California, about 100 miles south of the University. All three divisions are teaching units, presenting lecture and laboratory courses, and all take regular part in undergraduate teaching and graduate instruction leading to the degrees of A.M. and Ph.D. Most Stanford ichthyological work is done at the Museum and at the Marine Station.

At the Marine Station, ichthyological work is in the hands of Dr. Rolf Ling Bolin, Professor of Marine Biology and Oceanography, and Assistant Director of the Station. Professor Bolin currently gives the department's course in elementary ichthyology every summer at the Station and supervises the work of his group of graduate students there. Most of the latter are working on problems in marine ichthyology and fishery biology. Professor Bolin's own research has concerned especially the systematics of the Cottidae and Myctophidae, and he is now at work on a world monograph of the latter group. The Station maintains a small oceanographic vessel, the "Tage."

At the Natural History Museum, ichthyological work is guided by Dr. George Sprague Myers, Professor of Vertebrate Biology and Curator of Zoölogical Collections, and Dr. Donald Eugene Wohlschlag, Assistant Professor of Biology. Professor Myers gives courses in general vertebrate phylogeny, zoögeography, and herpetology, in addition to one in advanced systematic

ichthyology, and supervises graduate students in systematic ichthyology and herpetology. In addition he is chief curator of zoölogical collections in the Museum. Professor Wohlschlag currently gives courses in biometry, limnology, conservation, and fishery biology, and supervises graduate students intending to enter fresh-water fishery biology. Miss Margaret Hamilton Storey, Assistant Curator of Zoölogical Collections, and who gives our course in Museum Methods, is in direct charge of curatorial work in zoölogy, of the Museum's zoölogical library, and of editorial work on the Bulletin.

There are two Museum sections other than Zoölogy: Entomology (Professor Gordon Floyd Ferris, in charge); and the Dudley Herbarium (Professor Ira Loren Wiggins, Director of the Museum, in charge). The Museum is devoted wholly to teaching and research. It maintains no exhibits.

The Museum's fish collection, begun by David Starr Jordan in 1891, is now one of the half-dozen most important in the world. While the number of specimens is not accurately known, there are probably something over 500,000 fishes. The collection has recently been enriched by the addition of large sections of the Bermuda and Pacific deep-sea and shore collections obtained by Dr. William Beebe, generously turned over to us by him. The fish collection was under the direct charge of Dr. Albert W. C. T. Herre, from 1928 until his retirement in 1946. In addition to the University's fish collection, the almost equally large collection of the California Academy of Sciences in San Francisco (40 miles north of Stanford) is available for research work, the two institutions having long maintained close relationships.

Under the leadership of David Starr Jordan, President and later Chancellor of the University, and of Professor Charles Henry Gilbert, Chairman of the Department of Zoölogy (later incorporated into the Department of Biology) many well known workers in systematic ichthyology were students at Stanford, among them Alvin Seale, John Otterbein Snyder, Edwin Chapin Starks, Albert W. C. T. Herre, Henry Weed Fowler, and Carl Leavitt Hubbs. Later, under the leadership of Professors Snyder and Starks, of Dr. Herre, and of Professor Tage Skogsberg at the Marine Station, R. L. Bolin and G. S. Myers were students. Among the more recent systematic ichthyologists who have studied at Stanford: Dr. Earl S. Herald (work on Syngnathidae; now in charge of the Steinhart Aquarium, San Francisco); Professor William A. Gosline (work on siluroids; now at the University of Hawaii); Miss Janet Haig (review of Eurasian Siluridae; now at the Hancock Foundation, Los Angeles); Dr. Martin R. Brittan (revision of *Rasbora*; now at San Diego State College); Professor Clark Hubbs (Clinidae; now at the University of Texas); Professor Harry W. Freeman (Agonidae; now at the University of South Carolina); and Dr. Fred H. Tarp (Embiotocidae; now at Contra Costa Junior College).

Graduate students now working on problems in systematic ichthyology at the Museum include: James Böhlke (Characidae); John C. Briggs (Gobiesocidae); Herman Adair Fehlmann (eel-like blennies); Robert R. Harry (Iniomi); Giles W. Mead (Clupeidae; young fishes); Norman J. Wilimovsky (berycoids; Arctic fishes).

Fishery biology and convervation have held an important place at Stanford ever since the work of David Starr Jordan on the International Fur Seal Commission in the 1890's. In 1910-12 Professor Gilbert ushered in the modern era of American fishery biology with his long-continued study of the life history of the sockeye salmon in British Columbia. Work of this type was continued by Professor Snyder and by Professor Willis Horton Rich, who guided fishery work at Stanford from 1927 until his retirement in 1950.

A large number of Stanford men, aside from Professors Gilbert, Snyder and Rich, have contributed notably to fishery work. Among them we may mention: Dr. W. F. Thompson, sometime Director of the School of Fisheries of the University of Washington, and of several fishery investigations; Mr. O.

E. Sette, Chief of the Pacific Oceanic Fishery Investigations, Honolulu; Mr. William C. Herrington, Special Assistant to the Undersecretary of State, for fisheries, in Washington; Dr. L. A. Walford, Chief of the Branch of Fishery Biology, U. S. Fish and Wildlife Service, Washington; Dr. D. V. Villadolid, Director of Fisheries of the Philippine Republic; Mr. V. E. Brock, Director of Fisheries for Hawaii; Mr. J. C. Marr, Chief of South Pacific Investigations, Fish and Wildlife Service, Stanford; and Messrs. A. C. Taft, in charge of inland fisheries, and R. C. Croker, in charge of marine fisheries, California Department of Fish and Game, San Francisco.

Among other Stanford men and women who have contributed much to fish or fishery work are: In the U. S. Fish and Wildlife Service: J. T. Barnaby, O. B. Cope, H. H. Eckles, Frances Felin, M. G. Hanavan, H. B. Holmes, S. G. Jewett, Jr., G. B. Kelez, M. J. Lindner, G. I. Murphy, G. A. Rounsefell, K. Stanton, Seton H. Thompson, Elizabeth Vaughan. In the California Department of Fish and Game: †P. Bonnot, Frances N. Clark, R. D. Collyer, Jr., *Brian Curtis, Anita E. Daugherty, W. A. Dill, D. H. Fry, Jr., H. C. Godsil, F. B. Hagermann, H. McCully, P. M. Roedel, *N. B. Scofield, W. L. Scofield, L. Shapovalov, H. G. Orcutt, J. H. Wales. In Washington State service: J. A. Craig. In teaching or research: P. Doudoroff, Laura Clark Hubbs (Mrs. Carl L. Hubbs), D. C. G. MacKay, H. C. McMillin, Masamitsu Oshima, Dixie L. Ray, E. Ray, V. M. Tanner. In Brazil: A. L. Gomes, Alba A. Maranhão. In Peru: A. Landa. In Venezuela: A. Fernandez-Yepez. In Costa Rica: J. Cardona-Cooper. In Mexico: R. S. S. Nuñez. In the F A O, Italy: H. Rosa. In the Philippines: P. R. Manacop, R. R. Medina, H. R. Montalban, I. A. Ronquillo, A. M. Sarenas F. F. Talavera. In Egypt: I. A. Aboul-Ela. In India: V. G. Jhingran, H. Lall Arora, R. R. Prasad. († = recently deceased; retired.)

Three governmental fisheries agencies maintain headquarters and laboratories at Stanford, the South Pacific (U. S. coast) Investigations of the Fish and Wildlife Service, under Mr. Marr; the Western Fresh-water Investigations of the same Service, under Dr. O. B. Cope; and certain research projects of the California Division of Fish and Game. Cooperation of the University faculty and staff with these agencies is close, and Mr. Marr and Mr. Taft are honorary Lecturers in the Department. In addition an informal group consisting of all the fish and fishery workers and students in the Stanford area (called the "Fischverein") meets nearly every month (except in summer) to hear speakers and discuss matters of mutual interest. Meetings usually have an attendance of from 30 to 40 persons, an indication of the importance of the Stanford area in ichthyological work.

Unfortunately, funds to support publication of the Bulletin are very small and much more material is available than we can print. No really extensive papers can be published except with help from outside sources. Most of the fishery research of both faculty and students is the result of work done in connection with governmental agencies, and the results are usually published by those agencies. For this reason, relatively few papers on fishery biology have appeared in the Bulletin.

DESCRIPTION OF A NEW AUCHENIPTERID CATFISH OF THE GENUS PSEUDEPAPTERUS FROM THE AMAZON BASIN

By James Böhlke

Upon comparing a specimen of the auchenipterid genus *Pseudepapterus* from the Rio Negro with a specimen identified as *Pseudepapterus hasemani* (Steindachner, 1915, p. 68) from the Peruvian Amazon, it was immediately evident that the two forms were not the same species. As the generic status of *Pseudepapterus* as distinct from *Auchenipterus* is still subject to considerable doubt and a decision must await the accumulation of more material, the Rio Negro specimen has also been compared with specimens or descriptions of all the species included by Gosline (1945, p. 14) in *Auchenipterus*.

The new species has a higher anal ray count and a lower ventral ray count than any described species of *Auchenipterus*, and a lower pectoral and ventral ray count than *Pseudepapterus hasemani*.

Pseudepapterus cucuhyensis, new species
Figure 1

Holotype: SU 16788, from a sandbank at Cucuhy on the Columbian border, Rio Negro, Brazil; collected by the late Dr. Carl Ternetz, February 14, 1925.

Description: Measurements in thousandths of standard length, counts, and the important proportions are presented in Table 1. These are accompanied by a comparison with Steindachner's description of *Pseudepapterus hasemani* and a specimen also identified as that species from the upper Amazon in Peru.[1]

Body elongate, very compressed, its greatest depth occurring along the anterior portion of the anal fin and contained 4.6 in standard length. Least depth of caudal peduncle 2.0 in head, 10.1 in standard length. Head short, its dorsal aspect concave, its length 5.0 in standard length. Head width 1.9 in head length. Gape short, failing to reach anterior margin of eye; lower jaw included. Eye large, placed rather low on head, its horizontal diameter greatest, 0.9 in snout, 3.0 in head. Interorbital convex, slightly wider than snout length, equal to eye, 2.9 in head. Gill rakers long and slender, 7+11 on the first gill arch.

All barbels reaching at least slightly past anal fin origin, the maxillaries shortest, the inner mandibulars longest. Pectoral pore present, moderate in size. Pectoral spine serrated along its inner edge, the serrations directed proximally. Longest pectoral rays reaching beyond anterior end of ventral base when the fin is appressed. Longest ventral rays reaching beyond anal fin origin; inner ventral rays not connected across midventral surface of body. Dorsal fin very short and low, the spine unserrated. Adipose fin present, inserted far posteriorly. Procurrent caudal rays numerous, connected by a membrane, resembling the condition found in the pygidiid genus *Ochmacanthus*, although not as extensive.

Lateral line present, dendritic in form, with short vertical branches given off at inconstant intervals.

[1] SU 34211; Ambyiacu River, near Pebas, Peru; collected by W. G. Scherer, July 31, 1937.
This specimen is at variance with Steindachner's description of *Pseudepapterus hasemani* in several respects, i.e., in the placement of pectoral and ventral fins, but is here, at least provisionally, identified with that name.

No. 1

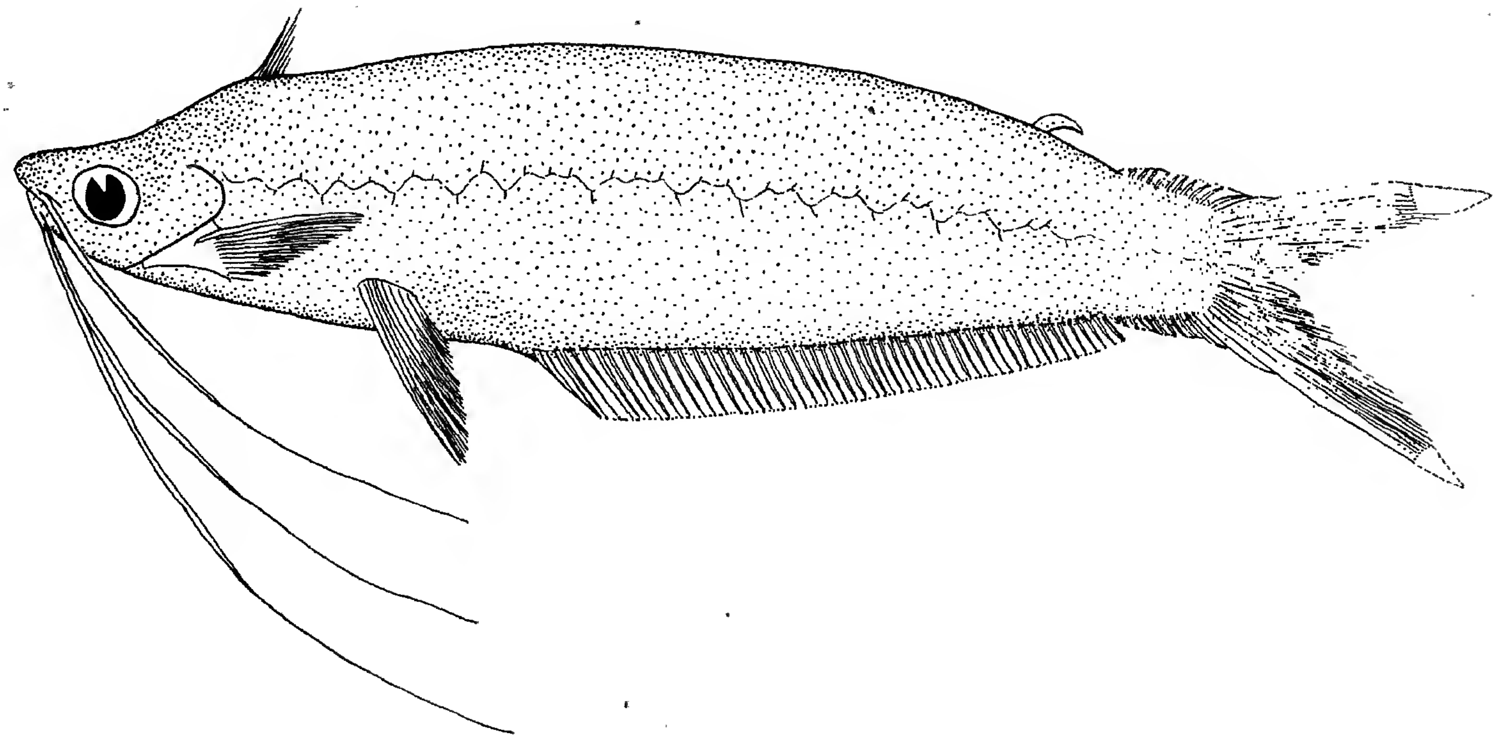

FIG. 1. Holotype of *Pseudepapterus cucuyensis*, SU 16788, 52.5 mm. standard length.
(Drawn by Miss Catherine S. Werner.)

Color in alcohol nearly uniformly light tan. Melanophores sprinkled more or less evenly over entire sides of fish, becoming more dense on the dorsal surface of the head.

This new species differs from *Pseudepapterus hasemani* in having a larger eye, and fewer rays in the pectoral and ventral fins.

1a. Ventrals I,11 or I,12; pectorals I,13 or I,14......*P. hasemani* Steind.
2a. Ventrals I,8; pectorals I,10..............*P. cucuhyensis*, new species

Table 1. Proportions and Counts of Specimens of *Pseudepapterus*
("length" is standard length)

	P. hasemani (after Steindachner)	Peruvian specimen	*P. cucuhyensis*
Length................................	93.0	59.5	52.5
The following are in thousandths of length:			
Length of head........................	182	218	200
Width of head.........................	104	113	105
Depth of body.........................	195	218	219
Depth of caudal peduncle..............	104	92	99
Length of caudal peduncle.............	104	101	107
Tip of snout to dorsal origin.........	169	202	210
Tip of snout to base of ventrals......	260	303	324
Eye diameter..........................	52	42	67
Length of snout.......................	52	67	63
Width of interorbital.................	78	84	69
Length of maxillary barbel............	390	445	410
Length of inner mandibular barbel.....	532	538	505
Length of outer mandibular barbel.....	390	462	419
Length of ventral fin.................	149	143	152
Length of pectoral fin................	182	168	162
Counts:			
Dorsal................................	I,5-6	I,5	I,5
Anal..................................	3/54	3/56	3/54
Pectoral..............................	I,14	I,13-I,13	I,10-I,10
Ventral...............................	I,11	I,12-I,12	I,8-I,8
Proportions:			
Head in length........................	5.5	4.6	5.0
Body depth in length..................	5.1	4.6	4.6
Peduncle depth in head length.........	1.8	2.4	2.0
Peduncle depth in length..............	9.6	10.8	10.1
Peduncle length in head length........	1.8	2.2	1.9
Peduncle length in length.............	9.6	9.9	9.4
Eye diameter in snout length..........	1.0	1.6	0.9
Eye diameter in interorbital width....	1.5	2.0	1.0
Eye diameter in head length...........	3.5	5.2	3.0
Snout length in head length...........	3.5	3.3	3.2
Interorbital width in head length.....	2.3	2.6	2.9
Maxillary barbel in length............	2.6	2.2	2.4
Inner mandibular barbel in length.....	1.9	1.9	2.0
Outer mandibular barbel in length.....	2.6	2.2	2.4
Snout to dorsal origin in length......	5.9	5.0	4.8
Snout to ventral base in length.......	3.9	3.3	3.1
Length of ventrals in head length.....	1.2	1.5	1.3
Length of pectorals in head length....	1.0	1.3	1.2

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REMARKS ON CLIMATOLOGY

A. E. Parr

It is obviously impossible to draw any clear and absolute line of demarkation between climatology and meteorology; the two subjects occupy too much ground in common. Until a very few years ago most of us, nevertheless, had a perfectly clear idea of what we meant when we spoke of climatology as a separate and special field of study. We knew it as we know a path we have followed for years, without being able to reduce it to an equation in geographic coordinates--perhaps even without being able to describe it. But still we were able to follow it again and again without any danger of getting lost. Today our path to climatological knowledge has been confused by a number of newly erected road signs all bearing the same name and all pointing in different directions. One might almost suspect that it had been done deliberately, in order to confuse the "invading" sciences which come in search of the knowledge they need for the solution of their own problems.

Before this confusion came about I believe most of us looked upon meteorology as the analysis and climatology as the synthesis of our knowledge of atmospheric events. Meteorology concerned itself with the explanation of the single event or of the individual phenomenon moving through space and time. Climatology dealt with the integration of these events, and of their effects, within fixed areas. The word integration is used with intention. Climate is not simply the sum or mean of the variables we call weather-conditions. It also expresses the normal pattern of variation, both in time, in space, and in the sequence of the variations themselves.

While dynamic meteorology moved forward with great strides, there was a constantly growing need for climatological knowledge which received almost no support and very little attention except from a small minority composed to a large extent of members recruited from other sciences. When the demand finally became too widespread and too insistent to be disregarded, meteorology showed its adaptability and good intentions by giving new names (all containing the word climatology) to a large number of its meteorological activities. Thus it might seem to an outsider as though meteorology were attempting to draw the fair wind blowing for climatology without changing meteorology's own course or taking on any new ports of call.

Most of the subjects which are now discussed under some climatological name or other would, only a few years ago, have been regarded as problems of meteorology pure and simple. What we are witnessing apparently is simply a gradual reclamation of the name Climatology for the entire subject of Meteorology, now that the older name has been found to possess what almost amounts to a popular appeal. But there is little indication that climatology, as we knew it quite recently and as we think of it in the natural sciences, will receive any more than the stepchild's share of attention which is all it has received from the students of the atmosphere since the introduction of dynamic meteorology.

The reasons offered for this avoidance of a difficult but urgently needed branch of research are twofold. One does not know what to do and, besides, it can't be done. While there may be a grain of truth in each of these complaints there is not an adequate excuse for inaction in either.

Whenever a suggestion is made to have meteorologists and climatologists design and initiate a large-scale program of climatological research, the point is immediately raised that one must first find out from the other sciences and technologies what kinds of climatological information is needed, before such a project can be properly planned and carried out. This at first sounds fair and reasonable, but when we try to obtain the specifications from the natural sciences we almost always run into a blank wall. Only in commerce, industry, and engineering does it seem possible to tell exactly what is wanted, and even here only under the simplest circumstances. Unless we are going to accept that nothing significant can be undertaken, except in narrow specific fields, we must conclude, therefore, that there is something wrong about the reasoning which leads us to wait for other sciences to tell us what climatology should do.

At this point it may be useful to consider another philosophical distinction between the meteorological and the climatological approach. By a rough generalization I believe we might define meteorology as the exact-science aspect, and climatology as the natural-science aspect of the study of the atmosphere. Among meteorologists there would seem to be a tendency to deny that anything useful and significant can be accomplished until and unless it can be done with the rigorous precision, completeness, and simplicity of mathematical equations. But to a natural scientist this would be the same as to say that it would be no use surveying the fauna and flora, the soils and rivers of a landscape, until the results can be stated in numerical tables and expressed in mathematical formulae--which means never. The meteorologists tend to forget that the study of the atmosphere is also part of the survey of the landscape, which must always remain in a large and fundamental sense a descriptive and qualitative study, because a landscape is too complex ever to find a total expression within the limited terms of the exact sciences.

Returning to our difficulties in finding out what meteorological information is wanted by others, we now realize that those who can tell us of their needs are generally the people who are able to base their own activities largely on the methods of fairly precise calculation and who are therefore primarily concerned with the relatively exact scientific aspects of meteorology. But for the natural sciences as a whole, including all aspects of pure and applied ecology, public health, anthropology, geology, and many other subjects, it is impossible to become specific about their needs except in very limited and special cases. And the fault, I believe, lies with climatology's failure to do its duty by its own initiative.

If the botanists, zoologists, and geographers had failed to undertake the tremendous task of classifying the animals and plants of the world and surveying their distribution until somebody else told them what plant or animal they wanted to find out about, what would the state and the prospects of economic entomology, the plant industries, agriculture, fisheries, and conservation be today? In fact the economic entomologist would not even be able to say what insect he wanted to find out about because nobody would know what insects were to be found or how to tell them apart. This, I submit, is exactly the quandary in which the natural sciences find themselves today, when they are asked to tell the climatologists what they want, because climatology has not given them the necessary information to go on.

If we are ever going to advance except at a snail's pace the students of the atmosphere must therefore take the initiative for the next step themselves. It seems obvious to me that what we need is a general meso- and micro-climatological survey of our entire country against which the other natural sciences, both pure and applied, can compare the results of their own surveys and observations. This, of course, is where we learn that it can not be done. But the reason we hear that statement is, in my opinion, simply that meteorology, in its preoccupation with the introduction of exact mathematical methods, has almost totally neglected the development of an adequate system of qualitative classification for climatology as a natural science.

I am not a meteorologist so I am quite incompetent to prepare a system of classification myself. But perhaps I can point to some useful parallels in subjects I know a little more about. When we describe a species in zoology, say a species of herring, we first examine all the features of the entire fish. Whenever possible we do it with a couple of dozen or even a couple of hundred specimens. We then give a full account of the entire appearance of the species, in all its details, but from this account we lift out and earmark separately just a very few so-called diagnostic characters. Perhaps a single character will suffice. And from there on all we have to look for is the presence of these few characters in order to record the occurrence of the species in space and in time. Only if we have reason to suspect that we are running into a previously unknown species, which might differ by other characters, do we have to check again with our complete description. Or if we want to refine our observations so as to record them in subspecific or racial terms. And from the features which are not diagnostic of the species but common to many of them, we draw our definitions of a hierarchy of higher and higher systematic groups, which, in reverse, enable us to arrive quickly and easily at the definition of any species we may be looking for. The role of this qualitative system in the natural sciences is in many ways similar to the role of the mathematical system in the sciences which claim to be more exact. In application to any concrete problem your measurements are substituted for the variables in your equation and the specimens for the generalizations of the qualitative definitions of the system.

I do not claim that climatology is entirely without any system of classification. On the contrary there have been some very notable advances made both in this country and elsewhere. But by comparison with the systems already developed in the other natural sciences, and in the exact sciences too, for that matter, the climatological system is still in a most rudimentary state. And

s is probably the main reason why any large-scale climatological research project is so quickly declared to be impossible.

Nevertheless, it would seem to a layman that the development of a more adequate system of climatological classification should be a comparatively easy undertaking. Easy enough so that it could be carried out as part of the larger survey in which it would find application, and would not have to be undertaken separately and in advance of the development of greater plans. If, for example, we find that climatic conditions in the deciduous forests of the northeastern United States usually conform to a certain general pattern of diurnal and seasonal variations, this pattern becomes part of the generic description of eastern deciduous forest climates, and a few special measurements at critical times and under the proper conditions are all that will be required in order to determine and to give an account of conditions in any specific forest within the region. Similarly, the length and diagnostic characters of a herring are all we need to have in order to know its other dimensions and characteristics, which can then be derived from the description of the species and the genus. Perhaps the diagnostic characters in climatology may prove to be relative rather than absolute. The information we need may be the difference between a few measurements made in the forest and in the open nearby under certain conditions of observation, rather than, for instance, the summer maximum or winter minimum temperature in the forest itself. If we now extend our comparison to the climatic conditions observed in the evergreen forests we will find that they conform to a different pattern of diurnal and seasonal changes, especially during the winter, but that they also show great similarities with the deciduous forest climates, particularly in the summer. These similarities we can then transfer from the generic descriptions of northeastern deciduous forest climates and northeastern evergreen forest climates to the family definition of northeastern forest climates in general. Each time we establish a higher classification in the hierarchy of our system, after adequate tests, we reduce the need for extensive observations and repetitive descriptions on lower levels. And it would seem particularly true that a determination of the diagnostic characters of the specific types of micro- and meso-climates would so enormously reduce the number of data required that it would bring entirely within the realm of practical possibility the task of making such a climatological survey as I have already suggested.

Reasoning by analogies drawn from a different field of study is always an awkward process and probably the hypothetical illustrations I have tried to suggest may seem very crude to you. But there is nothing crude about a system of classification such as that developed in zoology, which today enables us to identify and tell apart, without any waste of words or needless observations, more than half a million species of insects, in spite of all the individual variations and anomalies to be found in the single specimens. If the students of the atmosphere generally would learn to take a similar systematic attitude towards climatology as a chapter of natural history, using qualitative classifications to reduce the need for quantitative measurements, nothing in the task of making a comprehensive survey of our climates would seem impossible to them today, any more than it seemed impossible for the entomologists to survey our myriad insect life.

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Classification, Zoogeography and Evolution of the Fishes of the Cyprinoid families Homalopteridae and Gastromyzonidae

By

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CLASSIFICATION, ZOOGEOGRAPHY AND EVOLUTION OF THE FISHES OF THE CYPRINOID FAMILIES HOMALOPTERIDAE AND GASTROMYZONIDAE.*

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CONTENTS.

*Part of thesis submitted for the Research Degree of M.Sc., of the Madras University.

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I.—INTRODUCTION.

The Homalopteridae and Gastromyzonidae, which are found in the swift currents of the torrential streams in South Eastern Asia, constitute two remarkable families of Cyprinoid fishes. Habitudinal segregation has induced a great variety of adaptive modifications in them. In 1932, Hora gave an account of the "Classification, Bionomics and Evolution of the Homalopterid Fishes" and subdivided the family Homalopteridae (Hora, 1932) into two groups characterised by a number of well defined morphological features. From a study of the material available to him in the various museums of Europe and the Indian Museum at Calcutta, he was led to conclude that the family is polyphyletic in origin, the Homalopterinae having been evolved from the Cyprinidae and the Gastromyzoninae from the Cobitidae. The two subfamilies thus constituted were distinguished from each other by the number of unbranched rays in the paired fins, the nature of the subtemporal fossae and that of the basipterygium. It was also pointed out that the superficial resemblance between the Homalopterinae and Gastromyzoninae was due to similarity of life habits. He had limited material for a morphological study of the aforesaid characters in the seventeen genera to which about 48 species of the family were assigned.

Since then, considerable advance has resulted in our knowledge of these fishes, which has made a critical review of the group desirable once again. Moreover, such a revision is found essential for bringing together the scattered literature and discussing the geographical distribution and evolution of these fishes in the light of recent researches.

In the present work an attempt is also made to clarify the relationships of the various genera and subgenera, which in some cases, has involved a revision of the generic limits of certain genera. For the first time all the known genera and species are treated at length, and synoptic keys to their identification, with short descriptions of genera wherever necessary and notes on species are given. The intra-relationships, zoogeography and evolution of both the families are dealt with in detail. Recent researches tend to show that the Gastromyzonid fishes have evolved independently in South China and in Borneo. Further evidence in favour of this hypothesis is elaborated here.

One genus and one species are described as new and in addition, the correct systematic position of a number of previously known species has been determined. References later than 1932 are given under each genus and species. The bibliography appended at the end contains all recent literature and for the earlier works, Hora (1932. p. 228-230) may be consulted.

My greatest debt of acknowledgment is due to Dr. S. L. Hora, Director, Zoological Survey of India, for suggesting me this problem and for affording me all facilities to work in the Laboratories of the Zoological Survey of India. I am also greatly indebted to him for constant help and guidance in carrying out this work. My heartfelt thanks are also due to Dr. L. S. Ramaswami of Central College, Bangalore, for making available to me his recent works on the cranial osteology of the Homalopteridae and Gastromyzonidae and to Mr. A. G. K. Menon for helping me in various ways.

II.—RECENT ADVANCES IN OUR KNOWLEDGE OF THE HOMALOPTERID AND GASTROMYZONID FISHES.

The considerable amount of work done during the past two decades has helped to give us a more or less clear picture of the systematics of these fishes. In dividing the Homalopteridae into two subfamilies, Hora (1932) pointed out that " The Homalopteridae are probably a polyphyletic family and it is likely that its members are derived from the Cyprinidae and Cobitidae and have come to resemble one another superficially under similar conditions of environment." Recently, he reviewed the systematic position of the family in the light of the opinions expressed in regard to the above view and after an examination of large collections in several American Museums (Hora, 1950) concluded that the assemblage of fishes usually grouped under the family Homalopteridae should be classified into two distinct families, Homalopteridae and Gastromyzonidae, on the same considerations as were advanced for constituting the previous division of the family into two subfamilies. The marked polyphyletism exhibited by the Gastromyzonidae has led to its division into two subfamilies *viz.*, Crossostominae and Gastromyzoninae. In the present revision it has been found that, for a satisfactory classification of these fishes, a still further division of the Gastromyzoninae is necessary, as those genera confined to the mainland of Asia (Southern China, Formosa and Indo-China) can be easily distinguished from those found on the island of Borneo. The two divisions proposed are Pseudogastromyzoni for the genera on the mainland of Asia and Gastromyzoni for those found on Borneo.

Since 1932, a large number of species and genera have been described under the composite family Homalopteridae. From 17 genera and 48 species referred to in Hora's monograph of 1932, their number has increased to 28 genera and about 84 species (Homalopteridae 53 species pertaining to twelve genera and Gastromyzonidae 31 species referrable to sixteen genera).

Three new genera have been described under the Homalopteridae since 1932. The genus *Travancoria* was described by Hora (1941,

from the Hill ranges of Northern Travancore. Chang (1944) described *Metahomaloptera* from Loshan and Omei in China. *Balitoropsis* was described by Smith (1945) from Peninsular Siam. The genus *Bhavania* was merged by Hora with *Homaloptera* in 1932, but he revived it in 1941. In addition to the new genus *Pseudohomaloptera* described here, Herre's subgenus *Neohomaloptera* (Herre, 1945), is raised here to the rank of a genus. A number of new species have been described from time to time under the previously known genera.

Among the Gastromyzonidae, five new genera and a number of species have been added to the previously known list. The new genera are *Liniparhomaloptera* Fang (1935), *Praeformosania* Fang (1935), and *Paraprotomyzon* Pell. & Fang (1935) from China. *Glaniopsis* Boulenger was shown to belong to the Gastromyzonidae by Hora and Jayaram (1951) and they have also described a new genus *Progastromyzon* from Borneo.

Hora and Law (1944) gave an account of the respiratory adaptations of the South Indian Homalopterid fishes. Chang (1946) made a comparative study of the girdles and adjacent structures in the Chinese Homalopterid fishes with special reference to adaptations to torrential streams. I have not seen this paper and I am, therefore, not in a position to say what conclusions Chang has arrived at regarding the phylogeny of these fishes. Law (1950) studied the scale structure in a number of Homalopterid and Gastromyzonid genera and expressed opinions regarding their relationships and phylogeny. He has opined that the genus *Homaloptera* is probably a heterogenous assemblage of forms and that " different forms of *Homaloptera* seem to have given rise to various types of Homalopterine genera."

The recent work of Ramaswami (1948, 1951) on the chondrocranial and cranial osteology of some of the Homalopterid and Gastromyzonid fishes has helped in confirming previous taxonomic findings as well as certain phylogenetic considerations. In 1948 he made a detailed study of two Homalopterids, *Bhavania* Hora and *Balitora* Gray, and a Gastromyzonid, *Gastromyzon* Günther and listed as many as 13 characters distinguishing these two groups of fishes. In one of the two recent contributions (seen in MS), he has made further observations on the skull of two more genera of the Homalopteridae *viz.*, *Homaloptera* van Hass., and *Lepturichthys* Regan and compared them with *Bhavania* Hora and *Balitora* Gray. From a comparative study of the skulls of these four genera he has confirmed that the Homalopteridae have had their origin from the Cyprinod stock, but, later diverged under different environmental conditions. He has also enumerated seven characters on which the Homalopteridae could be said to resemble the Cyprinidae and four important characters on which they differ from them.

III.—LIST OF HOMALOPTERID AND GASTROMYZONID FISHES AND THEIR DISTRIBUTION.

The following table, comprises the known genera and species of the families Homalopteridae and Gastromyzonidae. The species have been arranged under the respective genera in alphabitical sequence. A 'X'

indicates the region from whence the species has been recorded. A somewhat artificial geographical division of their range of distribution has been adopted for convenience. The ten distribution regions here recognised are :—(1) Peninsular India (Western Ghats), (2) North East India, (3) Burma, (4) Siam, (5) Malaya Peninsula, (6) Sumatra, (7) Java, (8) Borneo, (9) Indo-China and (10) China and Formosa.

List of Species	1	2	3		5	6	7	8	9	10
Family HOMALOPTERIDAE—										
I. Genus BHAVANIA Hora—										
*1. *Bhavania australis* (Jerdon).	×	—	—	—	—	—	—	—	—	—
II. Genus HOMALOPTERA van Hasselt—										
*2. *Homaloptera amphisquamata* Weber & Beaufort.	—	—	—	—	—	×	—	—	—	—
*3. *Homaloptera bilineata* Blyth.	—	—	×	—	—	—	—	—	—	—
*4. *Homaloptera gymnogaster* Bleeker	—	—	—	—	—	×	—	—	—	—
*5. *Homaloptera heterolepis* Weber & Beaufort.	—	—	—	—	—	×	—	—	—	—
*6. *Homaloptera* sp. nov.	—	—	—	—	—	—	—	—	×	—
*7. *Homaloptera leonardi* Hora.	—	—	—	—	×	—	—	—	—	—
8. *Homaloptera lineata* Smith.	—	—	—	×	—	—	—	—	—	
*9. *Homaloptera modesta* (Vincig.).	—	—	×	×	—	—	—	—	—	
*10. *Homaloptera modiglianii* Perugia.	—	—	—	—	—	×	—	—	—	
*11. *Homaloptera montana* Herre.	×	—	—	—	—	—	—	—	—	
*12. *Homaloptera ocellata* Van der Hoeven.	—	—	—	—	—	×	×	—	—	
13. *Homaloptera ophiolepis* Bleeker.	—	—	—	—	—	×	×	×	—	—
*14. *Homaloptera orthogoniata* Vaillant.	—	—	—	—	×	—	—	×	—	—
15. *Homaloptera ripleyi* (Fowler).	—	—	—	—	—	×	—	—	—	—
*16. *Homaloptera rupicola* & Mukerji).	—	—	×	—	—	—	—	—	—	—
17. *Homaloptera salusur* Bleeker.	—	—	—	—	—	×	×	—	—	—
18. *Homaloptera sexmaculata* Fowler.	—	—	—	×	—	—	—	—	—	—
*19. *Homaloptera smithi* Hora.	—	—	—	×	—	—	—	—	—	—
20. *Homaloptera stephensoni* Hora.	—	—	—	—	—	—	—	×	—	—
21. *Homaloptera tweedei* Herre.	—	—	—	—	×	—	—	—	—	—
22. *Homaloptera ulmeri* Fowler.	—	—	—	—	—	×	—	—	—	—
23. *Homaloptera vanderbilti* Fowler.	—	—	—	—	—	×	—	—	—	—

* An asterisk preceding the name of a species indicates that specimens have been actually examined by the author.

List of Species	1	2	3	4	5	6	7	8	9	10
II. Genus HOMALOPTERA van Hasselt—*contd.*										
24. *Homaloptera wassinki* Bleeker.	—	—	—	—	×	×	×	×	—	—
*25. *Homaloptera weberi* Hora.	—	—	—	—	—	—	—	×	—	—
*26. *Homaloptera zollingeri* Bleeker.	—	—	—	×	×	×	×	—	—	—
III. Genus NEOHOMALOPTERA Herre—										
*27. *Neohomaloptera johorensis* Herre.	—	—	—	—	×	—	—	—	—	—
IV. Genus TRAVANCORIA Hora—										
*28. *Travancoria jonesi* Hora.	×	—	—	—	—	—	—	—	—	—
V. Genus PSEUDOHOMALOPTERA, gen. nov.—										
29. *Pseudohomaloptera tate-regani* (Popta).	—	—	—	—	—	—	—	×	—	—
VI. Genus *Balitora* Gray—										
*30. *Balitora brucei brucei* Gray.	—	×	—	—	—	—	—	—	—	—
*31. *Balitora brucei burmanicus* Hora.	—	—	×	—	—	—	—	—	—	—
32. *Balitora brucei melanosoma* Hora.	—	—	×	—	—	—	—			
*33. *Balitora brucei mysorensis* Hora.	×									
*34. *Balitora maculata* Gray.	—	×	—	—	—	—	—	—	—	—
VII. Genus BALITOROPSIS Smith—										
35. *Balitoropsis bartschi* Smith	—	—	—	×	—	—	—	—	—	—
VIII. Genus SINOHOMALOPTERA Fang—										
36. *Sinohomaloptera hoffmanni* Herre.	—	—	—	—	—	—	—	—	—	×
*37. *Sinohomaloptera kwangsiensis* Fang.	—	—	—	—	—	—	—	—	—	×
IX. Genus HEMIMYZON Regan—										
*38. *Hemimyzon abbreviata* (Günther).	—	—	—	—	—	—	—	—	—	×
*39. *Hemimyzon acuticauda* (Fang).	—	—	—	—	—	—	—	—	—	×
*40. *Hemimyzon formosanum* (Boulenger).	—	—	—	—	—	—	—	—	—	×
41. *Hemimyzon sinensis* (Sauvage & Dabry).	—	—	—	—	—	—	—	—	—	×
42. *Hemimyzon yaotanensis* (Fang).	—	—	—	—	—	—	—	—	—	×
X. Genus LEPTURICHTHYS Regan—										
*43. *Lepturichthys fimbriata* (Günther).	—	—	—	—	—	—	—	—	—	×
44. *Lepturichthys güntheri* Hora.	—	—	—	—	—	—	—	—	—	×
*45. *Lepturichthys nicholsi* Hora.	—	—	—	—	—	—	—	—	—	×

* An asterisk preceding the name of a species indicates that specimens have been actually examined by the author.

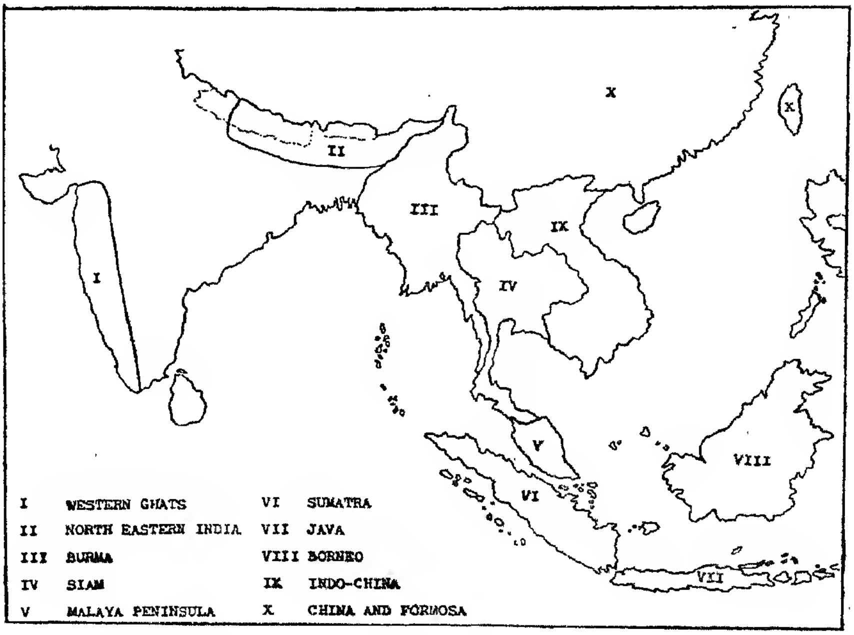
List of Species	1	2	3	4	5	6	7	8	9	10
XI. Genus SINOGASTROMYZON Fang—										
46. *Sinogastromyzon hsiashiensis* Fang.	—	—	—	—	—	—	—	—	—	×
47. *Sinogastromyzon intermedius* Fang.	—	—	—	—	—	—	—	—	—	×
*48. *Sinogastromyzon sanhoensis* Fang.	—	—	—	—	—	—	—	—	—	×
49. *Sinogastromyzon sichangensis* Chang.	—	—	—	—	—	—	—	—	—	×
*50. *Sinogastromyzon szechuanensis* Fang.	—	—	—	—	—	—	—	—	—	×
51. *Sinogastromyzon tonkinensis* Pell. & Fang.	—	—	—	—	—	—	—	—	×	—
52. *Sinogastromyzon wui* Fang.	—	—	—	—	—	—	—	—	—	×
XII. Genus METAHOMALOPTERA Chang—										
53. *Metahomaloptera omeiensis* Chang.	—	—	—	—	—	—	—	—	—	×
Family GASTROMYZONIDAE—										
Subfamily Crossostominae—										
I. Genus GLANIOPSIS Boulenger—										
*1. *Glaniopsis hanitschi* Boulenger.	—	—	—	—	—	—	—	×	—	—
II. Genus ANNAMIA Hora—										
2. *Annamia normani* (Hora).	—	—	—	—	—	—	—	—	×	—
III. Genus LINIPARHOMALOPTERA Fang—										
*3. *Liniparhomaloptera disparis* (Lin).	—	—	—	—	—	—	—	—	—	×
IV. Genus PARHOMALOPTERA Vaillant—										
*4. *Parhomaloptera microstoma* (Boulenger).	—	—	—	—	—	—	—	×	—	—
V. Genus VANMANENIA Hora—										
*5. *Vanmanenia caldwelli* (Nichols).	—	—	—	—	—	—	—	—	—	×
*6. *Vanmanenia stenosoma* (Boulenger).	—	—	—	—	—	—	—	—	—	×
VI. Genus PRAEFORMOSANIA Fang—										
7. *Praeformosania intermedia* Fang.	—	—	—	—	—	—	—	—	—	×
8. *Praeformosania lineata* Fang.	—	—	—	—	—	—	—	—	—	×
9. *Praeformosania pinchowensis* Fang.	—	—	—	—	—	—	—	—	—	×
VII. Genus FORMOSANIA Oshima—										
*10. *Formosania lacustre* (Steindachner).	—	—	—	—	—	—	—	—	—	×
VIII. Genus CROSSOSTOMA Sauvage—										
*11. *Crossostoma davidi* Sauvage.	—	—	—	—	—	—	—	—	—	×
*12. *Crossostoma fascicauda* Nichols.	—	—	—	—	—	—	—	—	—	×

* An asterisk preceding the name of a species indicates that specimens have been actually examined by the author.

List of Species	1	2	3	4	5	6	7	8	9	10
Subfamily Gastromyzoninae—										
Division I. PSEUDOGASTROMYZONI—										
IX. Genus PARAPROTOMYZON Pell. & Fang—										
*13. *Paraprotomyzon multifasciatus* Pell. & Fang.	—	—	—	—	—	—	—	—	—	×
X. Genus PSEUDOGASTROMYZON Nichols—										
14. *Pseudogastromyzon cheni* Liang.	—	—	—	—	—	—	—	—	—	×
15. *Pseudogastromyzon fangi* (Nichols).	—	—	—	—	—	—	—	—	—	×
16. *Pseudogastromyzon fasciatus* (Sauvage).	—	—	—	—	—	—	—	—	—	×
17. *Pseudogastromyzon fasciatus changtingensis* Liang.	—	—	—	—	—	—	—	—	—	×
18. *Pseudogastromyzon myersi* Herre.	—	—	—	—	—	—	—	—	—	×
19. *Pseudogastromyzon tungpiensis* Chon & Liang.	—	—	—	—	—	—	—	—	—	×
XI. Genus SEWELLIA Hora—										
*20. *Sewellia lineolata* Valenciennes.	—	—	—	—	—	—	—	—	×	—
XII. Genus BEAUFORTIA Hora—										
21. *Beaufortia kweichowensis* (Fang).	—	—	—	—	—	—	—	—	—	×
*22. *Beaufortia leveretti* (Nichols & Pope).	—	—	—	—	—	—	—	—	—	×
23. *Beaufortia liui* Chaing.	—	—	—	—	—	—	—	—	—	×
*24. *Beaufortia pingi* (Fang).	—	—	—	—	—	—	—	—	—	×
*25. *Beaufortia szechuanensis* (Fang).	—	—	—	—	—	—	—	—	—	×
26. *Beaufortia zebroidus* (Fang).	—	—	—	—	—	—	—	—	—	×
Division II. GASTROMYZONI—										
XIII. Genus PROTOMYZON Hora—										
*27. *Protomyzon borneensis* Hora & Jayaram.	—	—	—	—	—	—	—	×	—	—
*28. *Protomyzon whiteheadi* (Vaillant).	—	—	—	—	—	—	—	×	—	—
XIV. Genus PROGASTROMYZON Hora & Jayaram.										
*29. *Progastromyzon griswoldi* Hora & Jayaram.	—	—	—	—	—	—	—	×	—	—
XV. Genus NEOGASTROMYZON Popta—										
30. *Neogastromyzon nieuwenhuisi* Popta.	—	—	—	—	—	—	—	×	—	—
XVI. Genus GASTROMYZON Günther—										
*31. *Gastromyzon borneensis* Günther.	—	—	—	—	—	—	—	×	—	—

* An asterisk preceding the name of a species indicates that specimens have been actually examined by the author.

The above ten divisions are indicated in the following Map.



Text figure 1.—Map showing the areas of Distribution of the Homalopteridae and Gastromyzonidae.

IV.—KEY TO THE FAMILIES HOMALOPTERIDAE AND GASTROMYZONIDAE.

I. Two or more undivided anterior rays in the paired fins. Subtemporal fossae deep. Basipterygium with a lateral foramen and devoid of lateral horns ; a ligament connecting distal end of modified rib and lateral foramen of basipteygium .. .. .. *Homalopteridae.*

I. Only one undivided anterior ray in the paired fins. Subtemporal fossae shallow. Basipterygium without a lateral foramen but with a lateral horn ; a ligament connecting the medial process of modified rib with the lateral horn of the basipterygium .. *Gastromyzonidae.*

V.—FAMILY HOMALOPTERIDAE.

Fishes of the family Homalopteridae are small loach-like hill-stream fishes in which the body is moderately or greatly depressed and the ventral surface is flattened. The paired fins are horizontally placed and the number of unbranched rays in the paired fins are at least two. The outer rays of the paired fins are provided with adhesive pads on their ventral surface to help in adhering to rocks in the swift waters of the torrential streams. The eyes are small, dorso-lateral, with free orbital margins and are not visible from the ventral surface of the fish. The mouth is subterminal or inferior. The dorsal and anal fins are short. The body is covered with small cycloid scales which are absent on the head and on a part or whole of the

ventral surface. The lateral line is well marked and always extends to the base of the caudal fin. The gill openings are either greatly restricted, in which case they are situated above the bases of the pectorals or they are of moderate size extending to the ventral surface of the body for a short distance. Gill-membranes are united with the isthmus and the pseudobranchiae are absent.

Internal characters.—The subtemporal fossae are deep. The basipterygium is provided with a lateral foramen and there is no lateral horn. There is a ligament connecting the distal end of the modified rib and the region of the lateral foramen of the basipterygium.

In the upper jaw the opercular is elongated in a linear axis of the animal. The preopercular is reduced in size and the posterior process of the quadrate is large. In the lower jaw the sensory canal is on the mesial side of the angular. The tripus is Y-shaped, with one of its anterior limbs short and is connected with the interosseus ligament. The other limb articulates with the centrum of the fused third vertebra and the short posterior portion of the tripus is in contact with the air bladder. The divided air bladder is enclosed in a capsule which is formed by the dorsal ribs of the second and fourth vertebrae.

Distribution.—Peninsular India, North East India, Burma, Siam, Malaya Peninsula, Sumatra, Java, Borneo, Indo-China, China and Formosa.

Key to the identification of the genera of the family Homalopteridae.

I. Two anterior rays of pelvic fin simple—

A. Gill-openings small and situated entirely above base of pectorals .. .. *Bhavania.*

B. Gill-openings of moderate size, extending to the ventral surface for a short distance—

1. Rostral groove in front of mouth absent or very poorly developed. Rostral fold absent or very slightly developed—

a. One barbel at each corner of the mouth, in addition to two pairs of rostral barbels. Pelvics with two simple and 6 to 8 branched rays. Pectorals with 14 to 20 rays, 3 to 8 outer rays being unbranched .. .. .. *Homaloptera.*

b. Two barbels at each corner of the mouth, in addition to two pairs of rostral barbels [illegible] with 2 simple and 5 branched rays. [illegible] with 10 to 12 rays, 3 to 4 outer r[illegible] unbranched .. ..

2. Deep rostral groove in front of mouth present, o[illegible] hung by rostral fold—

a. Rostral barbels 7 or more, arranged in two series. *Travancoria.*

b. Rostral barbels 4, arranged in one row—

i. Lips simple, continuous at angles of mouth; lower lip followed by medially situated papillae. P. 8/12; V. 2/8 .. .. *Pseudohomaloptera.*

ii. Lips specially the upper strongly papillated. Lower lip not followed by medially situated papillae.

x. One barbel at each corner of the mouth—

y. Body and head greatly depressed; pelvic fin not reaching anal opening which is much nearer anal fin than the base of the pelvics. Pectorals beginning under eye, the rays 19 to 21 with 8 to 10 outer rays unbranched .. *Balitora.*

y′. Body cylindrical; head greatly depressed; pelvic fin extending beyond anal opening which is much nearer to base of pelvic than to anal fin. Pectorals beginning posterior to eye, the rays 14 with 4 outer rays unbranched .. .. ..

x′. Two barbels at each cornor of the mouth. (Pectorals with 20 rays, 7 to 8 outer rays being unbranched) .. .. .. *Sinohomaloptera.*

II. Three or more anterior rays of pelvic fin simple—

A. Pelvics free from each other, not uniting to form a disc like structure—

1. Two barbels at each corner of the mouth; tail stout and deep; least height of caudal peduncle greater than diameter of eye. Lips papillated .. *Hemimyzon.*

2. Three barbels at each corner of the mouth; tail long, slender; least height of caudal peduncle less than diameter of eye. Lips fimbriated .. *Lepturichthys.*

B. Pelvics united posteriorly to form a disc-like structure—

1. Gill-openings of moderate size, extending to ventral surface for short distance .. .. *Sinogastromyzon.*

2. Gill-openings small and situated entirely above base of pectorals .. .. *Metahomaloptera.*

Bhavania Hora.

1920. *Bhavania*, Hora, *Rec. Ind. Mus.*, **19**, p. 202.
1932. *Homaloptera*, Hora (in part), *Mem. Ind. Mus.*, **12**, p. 274.
1937. *Bhavania*, Hora, *Rec. Ind. Mus.*, **39**, p. 11.
1941. *Bhavania*, Hora, *Rec. Ind. Mus.*, **43**, p. 224.
1948. *Bhavania*, Ramaswami, *Proc. Zool. Soc. London*, **118**, p. 513. (Skull characters).

For the diagnostic characters of *Bhavania*, reference may be made to the key on page 182. Hora (1941) has redefined the genus and since then no new species has been described under it.

Genotype.—*Bhavania australis* (Jerdon).

Distribution.—Peninsular India (Hill ranges of Mysore, Nilgiris and Travancore).

General remarks.—Until recently, great confusion existed regarding the taxonomy of the genus *Bhavania* Hora. First described as *Platycara* by Jerdon (1848), the genus was for some time treated as *Homaloptera* by later ichthyologists. In view of the fact that *Platycara* was preoccupied (McClelland, 1839), and that the forms assigned to *Homaloptera* (*Platycara* of Jerdon) by some workers were quite different from the true *Homaloptera*, Hora (1920) proposed the name *Bhavania* to include two species, *viz.*, *B. australis* (Jerdon) and *B. annandalei* Hora. In 1932 he considered *Bhavania* as a synonym of *Homaloptera*, but in 1937 after examining further material from Peninsular India, the generic status of *Bhavania* was correctly determined. Later, in 1941 he placed *B. annandalei* in the synonymy of *B. australis*. At present the genus *Bhavania* is monotypic, being represented by the type and only species *B. australis* (Jerdon).

Bhavania, like the Chinese genus, *Metahomaloptera* Chang, possesses greatly reduced gill openings. Such a condition is parallelled in several genera of the Gastromyzonidae, such as, *Protomyzon* Hora, *Paraprotomyzon* Pell. & Fang, *Pseudogastromyzon* Nichols, *Sewellia* Hora, *Beaufortia* Hora, *Neogastromyzon* Popta and *Gastromyzon* Günther.

Bhavania australis (Jerdon).

1941. *Bhavania australis* Hora, *Rec. Ind. Mus.*, **43**, p. 225, pl. viii, fig. 1-3.
1941. *Bhavania australis*, Hora and Law, *Ibid*, **43**, p. 248.
1948. *Bhavania australis* Ramaswami, *Proc. Zool. Soc. London*, **118**, p. 515.
1950. *Bhavania australis*, Law, *Rec. Ind. Mus.*, **48**, p. 76, pl. iii, fig. 4.
1951. *Bhavania australis*, Silas, *J. Bombay Nat. Hist. Soc.*, **50**, (2), p. 330.

D. 2/7-9 ; A. 1 ; A. 1/5 ; A. 1/5-6 ; 6 ; P. 6-8/9-11 ; V. 2/7-8 ; C. 17-18 ; L. 1. 70-75.

Head contained 4·3 to 5·4 in standard length and 5·1 to 6·5 in total length. Depth of body 6·45 to 9·3 in standard and 8 to 11 in total length. Head about as long as broad. Diameter of eye contained 3·88 to 5·59 in head ; 1·94 to 3·19 in snout and 1·38 to 2 in inter-orbital space. Least height of caudal peduncle contained 1·5 to 2·2 in its length.

Locality.—Peninsular India (Hill ranges of Msyore, Nilgiris and Travancore).

Specimens examined :—

Reg. No.	*Locality.*	*Donor or collector.*	*No. of Specimens.*
F.9854/1	Stream on Nellimudu Estate, about 1,800 feet, Malabar Dt. Madras.	R. B. S. Sewell .	1 specimen.
F.9855/1	Cheerambadi, Nilgiris .	Ditto .	1 specimen.
F.9856/1	Stream at Nadgani, Nilgiris.	Ditto .	1 specimen.
F.9862/1	Stream on Calicut-Vayitri road at 29 miles. About 500 feet. Malabar Dt.	Ditto .	3 specimens.

Specimens examined—

Reg. No.	*Locality.*	*Donor or collector.*	*No. of Specimens.*
F.9863/1	Branch of Kabani and adjacent rice fields below Rassellas Estate, Manantoddy, about 2,500 feet, Malabar Dt.	R.B.S. Sewell	1 specimen.
F.9864/1	Cheerambadi, Nilgiris .	Ditto. . .	1 specimen.
F.13600/1	Kallar stream; foot of Ponmudi Hills, Western Ghats, S. Travancore.	S. Jones . .	1 specimen.
F.649/2	Ditto.	Ditto.	1 specimen.
F.650/2	Ditto.	Nat. Hist. Mus. Stanford.	4 specimens.
F.651/2	Ditto.	A. W. C. T. Herre .	3 specimens.

Homaloptera van Hasselt *emend* Van der Hœven.

1932. *Homaloptera*, Hora, *Mem. Ind. Mus.*, **12**, p. 274.
1933. *Homaloptera*, Smith, *J. Nat. Hist. Soc. Siam. Supplc.*, **9**, p. 78.
1934. *Homaloptera*, Herre, *Lingnan Sci. Journ. Canton*, **13**, pp. 285-296.
1934. *Homaloptera*, Fowler, *Proc. Acad. Nat. Sci. Philad.*, **86**, p. 98.
1937. *Homaloptera*, Fowler, *Ibid*, **89**, p. 152.
1940. *Homalopterula*, Fowler, *Ibid*, **91**, p. 379.
1941. *Homaloptera*, Hora, *Bull. Raffles Mus., Singapore.* No. 17, p. 61.

As a number of new species have been added under the genus *Homaloptera* since Hora's work on these fishes in 1932, a short redescription of the genus is given below :

Snout either broad and rounded (*Bhavania*-like), or long and pointed (*Helgia*-like). Mouth inferior, slightly arched and of moderate size. Lips continuous at angles of mouth. Three pairs of barbels, of which 4 are rostral and one situated at each angle of mouth. Gill openings oblique, extending to ventral surface for some distance. Body covered with small or moderately large scales, which are absent on head and part of ventral surface of fish. Pectorals may or may not overlap pelvics. Pectorals possess 14 to 20 rays of which 3 to 8 outer rays are simple. Pelvics with 8 to 10 rays of which 2 outer rays are simple. Caudal peduncle usually long and narrow. Caudal fin either emarginate or deeply forked, with the lower lobe longer than the upper. Dorsal commences in advance of pelvics, or opposite or slightly behind it.

Genotype.—*Homaloptera ocellata* Van der Hoeven.

Distribution.—Peninsular India (Annamalai Hills); Burma (Myitkyina District, Upper Burma; Meetan and Tenasserim, Lower Burma); Siam (Mekong at Chiengsen Kao, N. Thiland; Ronphibun; Khao Sabap at Banang; Pran river at Pak Tawan; Chiengmai; Tadi stream and Klong Pong at Ban Kiriwing, Nakhon Sritamarat; Bau Yai, Chantabun; Metang; Upper Bangpakong river; Tachin); Indo-China; Malaya Peninsula (Kula Tahan, Pahang, Mawai District, Johore); Sumatra (Lahat; Si Rambe, Lake Manindjan, Lau Borus, Laut Kawar;

Atchin, Lake Tawar; Matur, Pdaangscha Bovenlauden); Java (Bautam, Tjampea, Buitenzorg, Kediri, Batavia, Bandung, Parongkalong); Borneo (River Kapuas; River Mahakam; Sarawak).

General remarks.—Of all the twelve genera of the family Homalopteridae, *Homaloptera* van Hasselt, which is widely distributed and variable, forms more or less the generalised genus. In 1932, Hora assigned a heterogenous assemblage of 19 species to it and indicated the occurrence of another form at Perak in the Federated Malaya States. The same year he also recorded three species of *Homaloptera* from Siam *viz.*, *H. zollingeri* Bleeker, *H. smithi* Hora and *H. modesta* Vinciguerra.

Smith (1933) noted that *H. modesta*, originally described from Lower Burma was taken from three widely separated localities in Siam. *H. smithi* was first described from specimens collected from Peninsular Siam, but Fowler (1933) recorded it from Chieng Mai and Metang in Northern Siam, Bau Yai, north east of Bangkok and Chautaboon in South East Siam. Fowler also described two new species, *H. sexmaculata* and *H. septummaculata*, closely related to *H. smithi* from Chieng Mai, Northern Siam. Following Smith and Hora, *H. septummaculata* is treated here as a synonym of *H. sexmaculata*. In 1937, Fowler added another species of *Homaloptera*, *H. maxinae* to the fauna of Siam. This species was regarded by Smith, and Hora to be a synonym of *H. zollinegri* Bleeker.

In 1932, Tchang described *Homaloptera caldwelli chekianensis*, from Chekiang and next year figured and redescribed it. Fang (1935) has, however, shown it to be a synonym of *Vanamnenia stenostoma* (Boulenger).

Herre (1934) described a new species of *Homaloptera*, *H. hingi*, from Pok Fu Lam, Hong Kong, which Hora (1935) assigned to the genus *Nemachilus* of the Cobitidae.

In the results of the George Vanderbilt Sumatran expedition, Fowler (1940) reported the discovery of a new genus of Homalopterid fish and two new species of *Homaloptera*. The genus *Homalopterula* proposed by him to include the species *H. ripleyi* is provisionally assigned here as a synonym to the genus *Homaloptera*. The two new additions to *Homaloptera* are *H. vanderbilti* and *H. ulmeri*.

H. tweedei was described by Herre (1940) from Malaya Peninsula and Hora (1941) added another new species *H. leonardi* to the fauna of Malaya Peninsula. The year 1945 saw the addition of two other new species to the genus *Homaloptera*. Smith (1945) described *H. lineata* from Siam and Herre (1945) reported the discovery of another species *H. montana*, from the Annamalai Hills in Peninsular India.

Validity of the divisions proposed under the genus Homaloptera.—The great diversity of form and structure seen among the members of the genus *Homaloptera*, has resulted in attempts in the past to split it into several genera. Names such as, *Helgia*, *Homalopteroides*, *Chopraia*, *Homalopterula*, etc., have been proposed, and the validity of these generic names is discussed below.

Vinciguerra (1890) proposed the name *Helgia* for two species of *Homaloptera* from Burma, which he characterised as "Possessing long and pointed snout". An examination of the abundant material of

Homaloptera present in the collections of the Zoological Survey of India, Indian Museum, and a study of the characters of those species not represented here have revealed that among *Homaloptera,* there are all stages between *Helgia*-like forms with long pointed snout and *Bhavania* like forms with broad rounded snouts. It has been pointed out by Law (1951) that the scale of *H. modesta* differs from that of other species and may have generic significance. But the pointed snout, the character on which Vinciguerra based his genus, is not well defined when the genus *Homaloptera* is taken as a whole and as such, it has been thought best to supress the name *Helgia.*

Fowler (1905) created the genus *Homalopteroides* with *Homaloptera wassinki* Bleeker as its type. He characterised his genus as "Dorsal inserted well behind the ventrals", and thus distinguished it from *Homaloptera* (*sensu stricto*), where the "Dorsal begins in advance of the ventrals". This system of nomenclature has resulted in some confusion which is clarified here. Weber and Beaufort (1916) followed Fowler's classification and divided the genus *Homaloptera* into two subgenera *viz., Homalopteroides* Fowler and *Homaloptera* (*sensu stricto*). They also considered *H. wassinki* as the type of *Homalopteroides,* but at the same time included *H. ocellata* of Cuvier and Valenciennes in the *Homalopteroides.* This would make Fowler's *Homalopteroides* a synonym of *Homaloptera* (*sensu stricto*), since *H. ocellata* is the type of the latter. But, Hora (1932), after examining Cuvier and Valenciennes specimens of *H. ocellata* in the Paris Museum, found that they were really *H. wassinki.* He also pointed out that specimens assigned to *H. erythrorhina* and *H. pavonina* by Weber and Beaufort under *Homaloptera* (*sensu stricto*) were referrable to *H. ocellata* Van der Hoeven, the type of the genus. After examining all diagnostic characters of *Homaloptera,* the position of the dorsal fin in relation to the pelvics, seems to be the most suited character for a division of the genus into two subgenera. As such, in the present revision Fowler's divisions *viz., Homalopteroides* and *Homaloptera* (*sensu stricto*) are recognised.

In 1929, Prashad and Mukerji described the genus *Chopraia,* for a species from Northern Burma. *Chopraia* according to them differed from *Homaloptera* in possessing a broad head which is not greatly depressed, large eyes situated dorso-laterally in the middle of the head and the narrow branchial opening extending as far as the anterior margin of the pectoral fin on the ventral surface. *Chopraia* as defined by them is different from species of *Homaloptera* in Burma, but when the genus is taken as a whole, the above characters loose their diagnostic importance. They are so overlapping in the different species, that, as in the case of *Helgia,* no clear-cut division of the species can be made on the above mentioned characters. *Chopraia* is, therefore, treated as a synonym of the genus *Homaloptera.*

Fang (1930) considered *Sinohomaloptera* as a subgenus of *Homaloptera* and characterised it as "Barbels 2 at each angle of mouth ; a deep groove between snout and upper jaw ; 8 outer rays of pectoral and 3 (actually 2, *vide* Hora, 1932, p. 289) outer rays of the ventral simple". Subsequently from a study of the basipterygium and the modified rib, Fang (1930), raised *Sinohomaloptera* to the rank of a genus.

Homalopterula was proposed by Fowler (1940) for the Sumatran species *H. ripleyi*. *Homalopterula* is known chiefly "by the peculiar shape of the jaw, in combination with its truncated caudal and entirely naked medial under surface of the abdomen. It agrees with *Homalopteroides* with the backward insertion of the dorsal." The species is known from a single specimen which is not in a good state of preservation. Considerable variation exists regarding the nature of the caudal and presence or absence of scales on the ventral surface of the abdomen in species of *Homaloptera*. I have not examined this rare species, but from the figures provided by Fowler (*op. cit.*), it is obvious that the specimen is a *Homaloptera*. Moreover, as the characters are so overlapping, it has been thought best to consider *Homalopterula* for the time being as a synonym of *Homaloptera*.

Neohomaloptera Herre (1945), due to its marked differences from *Homaloptera*, is raised from the rank of a subgenus to that of a genus.

Key to the species of the genus Homaloptera *van Hasselt.*

I. Origin of dorsal behind origin of pelvic fin (*Homalopteroides*).

A. Lateral line scales 39 or less—

1. Pectoral longer than head, extending far on pelvics; P. 4-5/11-12; V. 2/6; scales in transverse series from base of pelvic fin 6-1-4½; back with six saddle shaped bands. All fins with irregular dark bands . *H. smithi.*

2. Pectorals shorter than head, extending to base of pelvic fin; P. 4/11; V. 2/6; scales in transverse series from base of pelvic fin 8½-1-5; a narrow dark stripe from head to base of caudal fin. Fins unmarked. *H. lineata.*

B. Lateral line scales 40 or more.

1. Lateral line scales 40 to 54.

a. Origin of dorsal nearer base of caudal than to tip of snout (L. 1.47; P. 6-7/10; V. 2/6; anal arises somewhat nearer end of pelvics than base of caudal; pelvics not reaching anus; pectorals slightly longer than head, reaching pelvics, caudal deeply emar- *H. wassinki.*

b. Origin of dorsal equidistant from tip of snout and base of caudal or nearer to tip of snout than to base of caudal.

i. Origin of dorsal equidistant from tip of snout and base of caudal.

x. Interorbital width more than diameter of eye; pelvics separated from anal opening by short distance. (L. 1.42-45) .. .. .. *H. rupicola.*

x'. Interorbital width equal or less than diameter of eye. Pelvics reach anal opening.

y. Interorbital width equal diameter of eye L. 1. 43-44 .. .. *H. indochinensis.*

y'. Interorbital width less than diameter of eye; L. 1. 44-46 .. .. *H. weberi.*

ii. Origin of dorsal nearer tip of snout than base of caudal.

x. Scales on back and sides carinated ; pectorals overlapping the pelvics. (L. l. 45 ; P. 5/11 ; V. 2/8 ; five round spots along dorsal surface ; the second from front encircling the base of dorsal fin ; fins marked with black bands ; snout marked with two pairs of longitudinal streaks radiating from the eye) .. *H. stephensoni.*

x'. Scales on back and sides not carinated. Pectorals separated from pelvics by considerable distance. L. 1. 40-51.

y. P. 2/12-14 ; V. 2/8-9 ; back with six or seven saddle like spots .. .. .. *H. sexmaculata.*

y'. P. 5-6/8 ; V. 2/6 ; back and sides with numerous irregularly disposed spots of various sizes and shapes. Three black spots on side of head below eye ; all fins barred with black .. .. *H. modesta.*

2. Lateral line scales 55 to 73.—

a. Pectorals with 7 to 8 simple rays—

i. Origin of pelvics equdistant from tip of snout and base of caudal. Height of dorsal $1\frac{1}{4}$ to $1\frac{1}{2}$ in head. Pelvics just reaching vent .. .. *H. vanderbilti.*

ii. Origin of pelvics much closer to tip of snout than to base of caudal. Height of dorsal 1 to $1\frac{1}{10}$ in head. Pelvics falling much short of vent which is situated midway between free margin of pelvics and anal fin .. .. .. *H. ulmeri*

b. Pectorals with 3 to 5 simple rays—

i. L. 1. 60 to 64 ; eyes 7 times in head 3 in interorbital space ; barbels twice as long as eye .. .. *H. modiglianii.*

ii. L. 1. 63 to 73 ; eyes 6 times or less in head ; less than twice in interorbital space. Barbels slightly longer or slightly shorter than eye—

x. Origin of dorsal before middle of length. P. 3-5/9-11.

y. Origin of anal much nearer base of caudal than that of pelvics. Ventral surface scaly between and behind pelvics. A triangular patch of scales before base of pelvices present or absent.

z. Ventral surface upto vent totally scaleless ; 43 scales between dorsal and occiput .. *H. ripleyi.*

z'. Ventral surface upto pelvics scaleless. A triangular patch of scales before base of pelvics present or absent.

Triangular patch of scales before pelvics present. 30 scales between dorsal and occiput. L. 1.63 to 70 ; head much longer than broad .. .. *H. gymnogaster.*

Triangular patch of scales before pelvics absent. 50 scales between dorsal and occiput. L. 1. 70 to 73 ; head about as broad as long .. .. *H. amphisquamata*

y'. Origin of anal equidistant from base of caudal and commencement of pelvics. Ventral surface scaly only behind pelvics .. *H. heterolepis.*

x'. Origin of dorsal behind middle of length P. 4/8. *H. montana.*

II. Origin of dorsal opposite or in front of origin of pelvic fin (*Homaloptera*).—

A. Scales on lateral line 36 to 48.—

1. Scales smooth without keels ; L. 1. 36-37 ; Pectoral extending beyond origin of pelvics .. .. *H tweedei.*

1 Scales provided with prominent keels ; L. 1. 45-48 Pectorals not reaching pelvics.—

a. Height 8 to $8\frac{1}{2}$ in total length ; Scales on upper surface with a single strong keel. Back with 6 obscure dark cross-bands ; upper caudal lobe with 2 to 3 oblique dark bands . . . . . . *H. zollingeri.*

b. Height $10\frac{1}{2}$ to $11\frac{1}{2}$ in total length ; scales on upper surface with a keel, the anterior ones with 2 to 4 short ones besides. 7 large brown spots on back, 4 of which are behind the dorsal ; sides with large brown unequal spots . *H. ophiolepis.*

B. Scales on lateral line 57 or more.—

1. Ventral surface except between and behind pelvics totally scaleless.—

a. Pelvics separated from anal opening by short distance. (L. 1. 64 ; P. 4/9-10 ; V. 2-7 ; anal commences closer to origin of pelvics than to base of caudal . *H. bilineata.*

b. Pelvics reaching or surpassing anal opening.—

i. L. 1. 63-67 ; P. 5/10-11 ; V. 2/8 ; large brown irregular blotches dorsally ; a brown streak from tip of snout to eye and continued behind it upto occiput ; another streak downwards across side of head . . . . . . *H. orthogoniata.*

ii. L. 1. 63-71 ; P. 6/10 ; V. 2/7 ; a series of 6 or 7 large brown yellow edged ocelli along back which may fuse into 3 large patches . . *H. ocellata.*

2. Ventral surface up to base of anal fin totally scaleless.—

a. L. 1. 57-60 ; P. 6/10 ; pelvics do not extend upto anal opening ; scales carinate ; eyes large, diameter contained 3·6 to 4·1 in head *H. leonardi.*

b. L. 1. 70-80 ; P. 7/10-11 ; pelvics extend for a short distance beyond anal opening ; scales smooth, without any trace of keels ; eyes small, diameter contained 8 times in head *H. salusur.*

Homaloptera smithi, Hora.

1932. *Homaloptera smithi*, Hora, *Mem. Ind. Mus.*, **21**, p. 286, pl. xi, fig. 3.
1934. *Homaloptera smithi*, Fowler, *Proc. Acad. Nat. Sci. Philad.*, p. 98.
1939. *Homaloptera smithi*, Fowler, *Ibid.*, p. 58.
1945. *Homaloptera smithi*, Smith, *Bull. U. S. Nat. Mus.*, **188**, p. 276, fig. 54.

D. 2/7 ; A. 1/5 ; P. 6/11-12 ; V. 2/6 ; L. 1. 37-39 ; L. tr. 6-1-$4\frac{1}{2}$.

Head contained 3·7 to 3·8 in standard length and 4·6 to 4·8 in total length ; depth of body 6·1 to 7·3 and 7·7 to 9 ; greatest width of head contained 1·3 in its length ; height at occiput 2 to 2·3. Snout broad, flat, obtusely pointed. Diameter of eye contained 4·4 to 5·1 in head ; 2·2 to 2·5 in snout and 1·3 to 1·9 in interorbital width. Least height of caudal peduncle contained two times in its length.

Locality.—Peninsular Siam ; Metang in Northern Siam ; Bau Yai north east of Bangkok and Chantaboon in South Eastern Siam.

Type specimen is preserved in the collection of the Zoological Survey of India, Indian Museum.

Specimens examined.—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 11293/1 (Type).	Khong Pong, Ban Kiriwong Nakon-Sritamarat ; Peninsular Siam.	H. M. Smith . .	1 specimen.
F. 11294/1	Do. . .	Do. . . .	3 specimens.
F. 11295/1	Tadi stream, Bau Kiriwong Peninsular Siam.	Do. . . .	2 specimens.
F. 652/2	Do. . .	U. S. Nat. Mus. . .	1 specimen.

Homaloptera lineata, Smith.

1945. *Homaloptera lineata*, Smith, *Bull. U. S. Nat. Mus.*, **188**, p. 277.

D. 2/7 ; A. 1/6 ; P. 4/10 ; V. 2/7 ; L. 1.37 ; L. tr. 8½. -1-5.

Head 4 and depth of body 6·75 in length. Width of head 1·5 in its length and 1·3 in its depth. Diameter of eye 3·5 in head ; 1·3 in snout and equal to interorbital space. Barbels very slender, inner rostral about 0·3 and outer about 0·5 diameter of eye. Least height of caudal peduncle contained 1·5 in its length.

Locality.—Mekong and Chiengsei Kao in Northern Siam.

Remarks.—*H. lineata* can be easily distinguished from other species of *Homaloptera* occurring in Siam in the possession of relatively fewer scales on the lateral line, the fin formulae and the characteristic colouration. Smith (*op. cit.*) observed : "The known specimens are apparently immature, a condition which would affect their body proportions and colourations, but not their squamation and fin formulae."

Homaloptera wassinki, Bleeker.

1932. *Homaloptera wassinki*, Hora, *Mem. Ind. Mus.*, **12**, p. 279.

1938. *Homaloptera wassinki*, Fowler, *Fisheries Bull, Singapore*, **1**. p. 55.

1941. *Homaloptera wassinki*, Hora, *Bull. Raffles Mus. Singapore*, **17**, p. 5.

D. 3/7 ; A. 2/5 ; P. 6/10-11 ; V. 2/6-7 ; L. 1. 47 ; L. tr. 6½-1-8½.

Head 4·3 in standard and 5 to 5·5 in total length. Depth of body 5·7 and 7. Diameter of eye 4·5 to 6 in head ; 3 in snout and somewhat less than two times in interorbital width.

The confusion regarding the specific limits of *H. wassinki* Bleeker, in relation to *H. ocellata* Cuvier & Valenciennes (Weber & Beaufort, 1916), has been referred to already (*vide supra*, p.187). A single specimen of *H. wassinki* in the collection of the Zoological Survey of India, Indian Museum, has been lost, most probably in the floods of the Varuna river at Banaras in September 1943.

Locality.—Malaya Peninsula; Sumatra (Lahat) ; Java (Bantam, Tjampea, Buitenzong, Kediri) ; Borneo (Rivers Kapuas and Mahakam, Sarawak).

Homaloptera rupicola (Prashad & Mukerji).

1929. *Chopraia rupicola*, Prashad and Mukerji, *Rec. Ind. Mus.*, **31**, p. 188, pl. viii, fig. 3.

1932. *Homaloptera rupicola*, Hora, *Mem. Ind. Mus.*, **12**, p. 288.

1951. *Homaloptera rupicola*, Silas, *Journ. Zool. Soc. India*, **3**, pp. 10-15.

D. 2/7 ; A. 2/5 ; P. 5/11, V. 2/6 ; L. 1. 42-45 ; L. tr. 12.

Head 4 in standard and 5 in total length ; width of head 1·5 in its length ; diameter of eye 4 in head and 1·8 in snout ; interorbital width slightly more than diameter of eye. Snout blunt, rounded and broad. Mouth with thick fleshy lips devoid of tubercles. Pectorals overlap pelvics. Least height of caudal peduncle contained about two times in its length.

Locality.—Myitkyina, Upper Burma.

Type specimen is preserved in the collection of the Zoological Survey of India, Indian Museum.

Specimens examined.—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 10879/1 Type	Rocky stream round about Kamaing, Myitkyina Dt., Northern Burma.	Dr. B. N. Chopra . .	1 specimen. Fins slightly damaged.
F. 10880/1	Do. . .	Do. . . .	3 specimens.
F. 10881/1	Sankha, a large hill stream midway between Kamaing and Mongang, Myitkyina Dt.	Do. . . .	30 specimens.
F. 10882/1	Sattan Chanag stream inside and near Pandawan Cane about 8 miles from Kamaing. Myitkyina Dt.	Do. . . .	1 specimen.
F. 10883/1	Small muddy stream along Kamaing, Jade Mines road, Myitkyina Dt.	Do. . . .	12 specimens.
F. 10884/1	Rocky stream about half a mile from Namma Rest House. Myitkyina Dt.	Do. . . .	7 specimens.
F. 10885/1	Small rocky stream round about Kamaing, Myitkyina Dt.	Do. . . .	7 specimens.

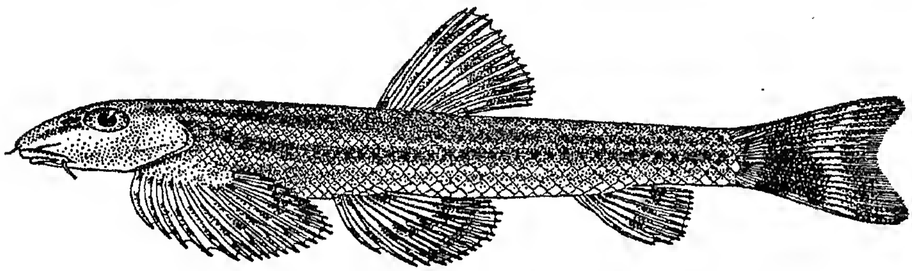
Homaloptera indochinensis, sp. nov.

(Text-figure 2.)

1951. *Homaloptera* sp. Silas, *J. Zool. Soc. India*, **3**, pp. 10-15.

D. 2/7/1 ; A. 1/5/1 ; P. 5/10/2 ; V. 2/7 ; C. 19 ; L. 1. 4 -44.

While describing a specimen of *Homaloptera* from Indo-China (*op. cit.*), it was pointed out that the form showed affinities to *Homaloptera rupicola* of Northern Burma and *H. weberi* of Borneo. Both on geographical grounds as well as on the differences it evinces from other species of *Homaloptera*, in the present revision it has been possible to specifically name it as a new species, *Homaloptera indochinensis* sp. nov. As already a detailed description of the specimen is given elsewhere (Silas, *loc. cit.*), only the diagnostic characters and a figure of the new species are given below :—



Text figure 2. Homaloptera indochinensis sp. nov. Lateral view. 1¾.

Head 4·7 in standard and 5·9 in total length. Depth of body 8·5 and 10·6. Width of head contained 0·6 in its length. Diameter of eye contained 4·5 in head and 2·1 in snout. Inter orbital width 1·95 in snout. Least height of caudal peduncle contained 2·1 times in its length. Pectorals overlap base of pelvics.

Type specimen is in the British Museum (1933-8·19·50).

Locality.—Indo-China (? Tonkin).

Homaloptera weberi, Hora.

1932. *Homaloptera weberi*, Hora *Mem. Ind. Mus.*, **12**, p. 284, pl. xi, fig. 2.

1951. *Homaloptera weberi*, Silas, *J. Zool. Soc. India*, **3**, pp. 10-15.

D. 2/7 ; A. 2/5 ; P. 5/11 ; V. 2/7-8 ; L. 1. 44-46.

Head contained 4·3 in standard and 5·5 in total length ; width of head 1·3 in its length. Diameter of eye 3·8 in head and 1·8 in snout. Interorbital width slightly less than diameter of eye. Least height of caudal peduncle contained 2·1 in its length.

Locality.—Akar River, Sarawak, Borneo.

Type specimen preserved in the British Museum.

Specimens examined.—

Register. No.		*Donor or Collector.*	*No. of specimens.*
F. 11292/1	Akar River, Sarawak, Borneo.	British Museum .	1 specimen.

Homaloptera stephensoni, Hora.

1932. *Homaloptera stephensoni*, Hora, *Mem. Ind. Mus.*, **12**, p. 281, pl. xi, fig. 1

D. 2/7 ; A. 2/5 ; P. 5/11 ; V. 2/8 ; L. 1. 45 ; L. tr. 5-1-3.

Head contained 4·6 in standard and 5·7 in total length ; depth of body 7 and 8·7. Width of head in front of pectoral contained 1·2 in its length ; height at occiput 1·7. Diameter of eye contained 4·3 in

length of head, 2·2 in snout and 1·2 in interorbital width. Least height of caudal peduncle contained 2·7 in its length.

Locality.—Upper Mahakam river, Borneo.

Type specimen preserved in Leyden Museum.

Homaloptera sexmaculata, Flower.

1934. *Homaloptera sexmaculata,* Fowler, *Proc. Acad. Nat. Sci. Philad.,* **86,** 98, fig. 47-48.

1934. *Homaloptera septummasulata,* Fowler, *Ibid.,* **86,** p. 99. fig. 49-50.

1945. *Homaloptera sexmaculata,* Smith, *Bull. U. S. Nat. Mus.,* **188,** p. 275.

1945. *Homaloptera septummaculata,* Smith, *Ibid.,* **188,** p. 275.

1950. *Homaloptera sexmaculata,* Hora, *Rec. Ind. Mus.,* **48,** p. 51.

D. 2/8/1 ; A. 1/5 ; P. 2/12-14 ; V. 2/8-9 ; L. 1. 42-51.

Head 4·33 to 4·75 and depth of body 5·8 to 7 in length. Width of head 1·2 to 1·25 in its length. Snout 2 to 2·75 in head. Diameter of eye 3·75 to 4·12 in head, 1·5 to 1·9 in snout and 1·33 to 1·5 in interorbital space. Width of mouth 4·25 to 4·35 in head.

Locality.—Meping at Chiengmai, Siam.

Remarks.—Speaking of the great similarity between *H. sexmaculata* and *H. septummaculata,* Smith (1945, p. 275) observed " The general pattern of colouration is practically identical in the two forms, and the only difference except in maculation appears to be in the lateral line scales, which number 42 to 46 in *H. sexmaculata* and 49 to 51 in *H. septummaculata.* It is probable that these two forms may represent a single species ". Recently after examining Fowler's material of the two forms in the Philadelphia Academy of Sciences, Museum Hora (1950) also expressed the opinion that they are con-specific. The juvenile condition of the known specimens may be responsible for the slight differences observed in these forms.

Homaloptera modesta (Vinciguerra).

1890. *Helgia modesta,* Vinciguerra, *Ann. Mus. Civ. Stor. Nat. Genova,* (2) **9,** p. 202, pl. ii, fig. 12.

1932. *Homaloptera modesta,* Hora, *Mem. Ind. Mus.,* **12,** p. 288.

1945. *Homaloptera modesta,* Smith, *Bull. U. S. Nat. Mus.,* **188,** p. 275.

D. 2/7 ; A. 6-7 ; P. 5-6/8 ; V. 2/6 ; L. 1. 47.

Head contained 3·75 to 4·5 in standard and 4·5 to 5 in total length. Head much longer than broad ; snout pointed. Width of head about length of head from tip of snout to posterior border of orbit. Length of snout 0·5 in head. Height at occiput slightly more than two times in length of head. Diameter of eye contained 4·25 in head ; 1·75 in snout and 1·25 in interorbital space. Depth of body contained 9 to 9·5 in total and about 8 in standard length. Least height of caudal peduncle contained 1·5 times in its length.

Locality.—Meetan, Lower Burma.

Specimens examined.—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens and state of preservation.*
F. 11040/1	Meetan, Lower Burma	Mus. Civ. Stor. Nat. Genova.	2 specimens. One of them is badly desiccated.

Homaloptera vanderbilti, Fowler.

1940. *Homaloptera vanderbilti*, Fowler, *Proc. Acad. Nat. Sci. Philad.*, **91**, p. 375, fig. 1-2.

1950. *Homaloptera vanderbilti*, Hora, *Rec. Ind. Mus.*, **48**, p. 51.

D. 2/7/1 ; A. 2/5/1 ; P. 8/9/2 ; V. 2/8 ; L. 1. 55-67.

Head contained 4 to 4·8 and depth of body 5·25 to 6 in length. Width of head 1·18 to 1·7 and snout 2 to 2·2 in head. Diameter of eye contained 5 to 7 in head, 2 to 3·75 in snout, and 1·6 to 3 interorbital width. Width of mouth contained 2·4 to 2·5 in head. Predorsal scales 34 to 35. Least depth of caudal peduncle 2·2 to 2·4 in head.

Locality.—Balanganga, in Tirpa river at base camp, 3600 feet elevation, Atjeh Province, Sumatra.

Remarks.—Hora (*op. cit.*) after examining specimens of *H. vanderbilti* and *H. ulmeri* stated: " *H. ulmeri* and *H. vanderbilti* may prove to be con-specific when further material becomes available ". I have not examined this species, but from Fowler's original descriptions and figures, I consider it best to treat *H. ulmeri* and *H. vanderbilti* as distinct species.

Homaloptera ulmeri, Fowler.

1940. *Homaloptera ulmeri*, Fowler, *Proc. Acad. Nat. Sci. Philad.*, **91**, p. 377 fig. 3-4.

1950. *Homaloptera ulmeri*, Hora, *Red. Ind. Mus.*, **48**, p. 51.

D. 2/7/1 ; A. 3/5/1 ; P. 7/8 ; V. 2/8 ; L. 1. 55-65.

Head 4·25 to 4·3 and depth of body 6·33 to 7 in length. Width of head 1 to 1·24 and snout 1·8 to 2 in head. Diameter of eye contained 5·25 to 6·2 in head, 3 in snout, and 2 to 2·25 in interorbital space. Width of mouth 2·75 to 3 in head. Predorsal scales 32 to 33. Least height of caudal peduncle 2·1 to 2·3 in head.

Locality.—Goepang River at Meloewak in Atjeh Province, Sumatra.

Homaloptera modiglianii Perugia.

1893. *Homaloptera modiglianii*, Perugia, *Ann. Mus. Civ. Genova*, **33**, (2) XIII, p. 245.

1916. *Homaloptera modiglianii*, Weber & Beaufort, *Fish. Indo-Austral. Archipel.*, **3**, p. 11.

1932. *Homaloptera modiglianii*, Hora, *Mem. Ind. Mus.*, **12**, p. 288.

D. 3/6 ; A. 9 ; V. 2/7 ; p. 5/9-10 ; L. 1. 60-64.

Perugia (1893), gave a short description of *H. modiglianii*, which Weber and Beaufort (1916) followed. As I have examined a specimen of this rare species, and since, there exists no detailed description of it, I am redefining it here.

Homaloptera modiglianii is a small slender loach in which the head and body are greatly depressed ; dorsal profile is slightly arched, it rises from tip of snout to hind end of occipital region, from whence it runs straight to the commencement of the dorsal and thence gradually slopes to the base of the caudal fin.

Head contained 5 to 5·5 and depth of body 8·75 to 9·25 in total length. Head longer than broad ; snout broad, flat, obtusely pointed. Snout slightly longer than half length of head and consequently the eyes are situated in posterior half of head. Height of head at occiput about half its length. Eyes dorso-lateral, of moderate size ; diameter contained 7 in head, 3·75 in snout, and 3 in interorbital width. Mouth inferior, cresent-shaped and bordered by thick plain lips which are continuous at angles, but interrupted widely in lower jaw. Barbels slightly longer than diameter of eye.

Caudal peduncle longer than deep, its least height contained 1·5 times in its length. Scales absent on head and anterior half of abdomen ventrally. Scales longer than broad, with a large structureless nuclear area, and a smaller number of circuli. Radii absent in apical and in adjoining lateral areas.

Dorsal commences closer to base of caudal than to tip of snout. Its origin slightly behind that of pelvics. Length of dorsal greater than depth of body beneath it and it is about as long as pelvics. Paired fins are flat and broad. Pectoral slightly pedunculate, with inner 1/3 vertical and outer 2/3 horizontal. Pectorals about as long as head and separated from pelvics by short distance. Pelvics fall much short of vent and their length is contained 0·75 in head. Anal shorter than dorsal. Caudal slightly emarginate, its lobes being equal. Colour in alcohol is yellowish, marmourated with brown. A black transverse band at base of caudal. Fins yellowish and immaculate.

Locality.—Sumatra (Si Rambe).

Specimen examined.—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 11296/1	Sumatra .	Mus. Civ. Stor. Nat. Genova.	1 specimen.

Homaloptera ripleyi, (Fowler).

1940. *Homalopterula ripleyi*, Fowler, *Proc. Acad. Nat. Sci. Philad.*, **91**, p. 379, figs. 5-7.

1950. *Homaloptera ripleyi*, Hora, *Rec. Ind. Mus.*, **48**, p. 51.

D. 3/7/1 ; A. 2/5/1 ; P. 3/10 ; V. 2/7 ; L. 1. 73.

Head 4·7 and depth of body 7·75 in length. Width of head 1·2 and snout 1·9 in head. Diameter of eye 6 in head, 3·25 in snout and 2 in interorbital width. Width of mouth 2·75 in head. Interorbital space 3 in head ; predorsal scales 43. Head and entire medial abdominal region scaleless back to vent. Height of dorsal 2 in head and anal 1·75. Least depth of caudal peduncle 2·2 in head.

Locality.—Geompang River, Meloewak in Atjeh Province, Sumatra.

Remarks.—Reference may be made to the discussion (*vide supra*, p. 188) for the relationships of Fowler's genus *Homalopterula*. Hora (*op. cit.*) after an examination of the type and only specimen of *H. ripleyi* stated : "....the only specimen of this species is not in a good state of preservation, so the characters could not be made out". Further material when obtained will throw more light on the systematic position of this species.

Homaloptera gymnogaster, Bleeker.

1916. *Homaloptera gymnogaster*, Weber and Beaufort, *Fish. Indo-Austral Archip.* **3**, p. 11.

1916. *Homaloptera lepidogaster*, Weber and Beaufort, *Ibid*, **3**, p. 14.

1932. *Homaloptera gymnogaster*, Hora, *Mem. Ind. Mus.*, **12**, p. 280.

D. 2/7-8 ; A. 2/6 ; P. 5-6/9-10 ; V. 2/7 ; L. 1. 63-70.

Head contained 5·5 and depth of body 7·75 in standard length. Length of snout greater than half length of head. Head longer than broad, its width contained 1·33 in its length. Eyes moderately large, its diameter contained 6·25 in head, and 1·5 in interorbital width. Predorsal scales 30. On ventral surface scales present between pelvics, and in a triangular patch before them.

Locality.—Sumatra (Lake Manindjau, river Anei near Kaju Tanam).

Specimens examined.—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 11297/1	River Anei near Kaju Tanam, Sumatra.	Zool. Mus. Amsterdam	1 specimen. Caudal damaged.

Homaloptera amphisquamata, Weber & Beaufort.

1916. *Homaloptera amphisquamata*, Weber and Beaufort, *Fishes Indo-Austral.* Archip., **3**, p. 12.

1932. *Homaloptera amphisquamata*, Hora, *Mem. Ind. Mus.*, **12**, p. 288.

1951. *Homaloptera amphisquamata*, Ramaswami, *Proc. Nat. Inst. Sci. India.* (in press).

D. 3/7 ; A. 3/4-5 ; P. 6-7/9-10 ; V. 2-3/6 ; L. 1. 70-73.

Head 4·7 in standard length and 5·5 in total length. Depth of body 7·2 and 8·5. Diameter of eye less than 5 in head, about 2 in snout and less than 2 times in interorbital space. Origin of dorsal behind that of pelvics, but is closer to tip of snout than to base of caudal. Ventral surface scaly only between and behind pelvics. Predorsal scales 50.

Locality.—Sumatra (Lau Borus, Karo Highlands).

Specimens examined.—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 11045/1	Lau Borus, Karo Highlands, Sumatra.	Zool. Mus. Amsterdam	3 specimens, of which one is slightly

Homaloptera heterolepis, Weber & Beaufort.

1916. *Homaloptera heterolepis*, Weber & Beaufort, *Fish. Indo-Austral. Archipel.* **3**, p. 12.

D. 2/7 ; A. 2/5 ; P. 4-5/8-10 ; V. 2/7-8 ; L. 1. 63-70 ; L. tr. 12-1-10.

Head 4·7 in standard and 5·6 in total length. Depth of body 6·4 and 7·6. Diameter of eye about 5 in head, 2·3 in snout and 2 in interorbital space. Origin of dorsal behind commencement of pelvics, and much nearer tip of snout than base of caudal. Pectorals much shorter than head, not reaching pelvics. Scales on abdomen only behind pelvics.

Locality.—Sumatra (Atchin, Lake Tawar).

Specimens examined.—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 11035/1	Lake Tawar, Sumatra	Zool. Mus. Amsterdam .	2 specimens.

Homaloptera montana, Herre.

(Plate I, figs. 1-2).

1945. *Homaloptera montana*, Herre, Journ. *Washington Sci. Soc.*, **20**, pp. 399 .
1950. *Homaloptera montana*, Hora, *Rec. Ind. Mus.*, **48**, p. 54.
1951. *Homaloptera montana*, Silas, *Journ. Bombay Nat. Hist. Soc.* **49**, p. 679.

D. 2/6 ; A. 1/5 ; P. 4/8 ; V. 2-3/6-7 ; L. 1. 72 ; L. tr. 16-1-12.

Known from the type and only specimen, *H. montana* was described by Herre (*op. cit.*) from the Anamalai Hills in Peninsular India. I have examined the type specimen received on loan from the Zoological Museum of Stanford University, U. S. A., and am redescribing it here with illustrations.

Head 4·8 and depth of body 9·6 in total length. Length of caudal and pelvic equal to that of head. Diameter of eye 4·3 in head, 2·8 in snout and 1·7 in interorbital width. Snout 2 and postorbital part of head 2·5 in head. Least depth of caudal peduncle twice in its own length.

Body slender, posterior half being laterally compressed ; dorsal profile little elevated ; eyes dorso-lateral ; snout descends steeply with rather flat tip. Mouth small, slightly arched ; barbels small and inconspicuous. Dorsal origin well behind that of pelvics and behind middle of length. Pectorals just reaching plevic base. Pelvics fall short of anus which is noticeably in advance of anal origin. Caudal nearly truncate. Head and entire ventral surface back to a little behind pelvic base scaleless.

Herre (*op. cit.*) gives the colour as " in alcohol brown, the under side yellowish ; 10 dark short bars across the back, but not extending back to the lateral line ; a poorly defined dark longitudinal stripe below the lateral line from the eye to the caudal base ; top of head very dark brown ; a blackish brown spot on ventral base ; caudal with a blackish blotch on its base, and another near its tip ; other fins all clear ".

Locality.—Puthutotam Estate, Anamalai Hills, South India.

Remarks.—*H. montana* throws some light as to the Malayan affinities of the fish fauna of Peninsular India. Recently Hora (1950) and Silas (1951) have discussed the Zoogeographical significance of the occurrence of this species in Peninsular India.

Homaloptera tweedei, Herre.

1940. *Homaloptera tweedei*, Herre, *Bull. Raffles Mus.*, **16**, pp. 7-8. pl. i, fig. 1.
1941. *Homaloptera tweedei*, Hora, *Ibid.*, **17**, p. 61.
1944. *Homaloptera tweedei*, Herre, *Proc. Biol. Soc. Washington*, **57**, p. 51.

D. 1/8; A. 1/4-5; P. 4/10; V. 2/7; L. 1. 36-37; L. tr. 4-5/3-3·5.

Head 3·4 to 3·55 and depth of body 6·6 to 6·8 in total ength. Diameter of eye 3·8 to 4 in head and about equal to that of interorbital space. Snout 2·6 in head. Interorbital space 1·5 in snout. Least depth of caudal peduncle 2·2 in its length.

Locality.—Mawai District, Johore, Malaya Peninsula.

Remarks.—*H. tweedei* is also characterised by the relatively large size of the scales, fewer rays in the pectoral fins, pectorals overlapping pelvics, larger eyes and the scaleless ventral surface up to the pelvics. For a complete diagnosis of the species reference may be made to Herre (1940, *loc. cit.*).

Homaloptera zollenger, Bleeker.

1916. *Homaloptera zollengeri*, Weber and Beaufort, *Fish. Indo-Austral. Archip.*, **3**, p. 14.
1932. *Homaloptera zollengeri*, Hora, *Mem. Ind. Mus.*, **12**, p. 280.
1937. *Homaloptera maxinae*, Fowler, *Proc. Acad. Nat. Sci. Philad.*, p. 152 figs. 52-53.
1945. *Homaloptera zollengeri*, Smith, *Bull. U. S. Nat. Mus.*, **188**, p. 274.

D. 2/8; A. 2/5-6; P. 4/9-10/1; V. 2/8; L. 1. 45.

Head 6 to 6·3 and depth of body 8 to 8·5 in total length. Diameter of eye 4·5 to 5·5 in head; and about 2 in interorbital width. Origin of dorsal ahead of pelvics. Scales on back and sides with a strong longitudinal keel. Pectorals separated from pelvics by a short distance.

Locality.—Siam (Upper Bangpakong river); Java (Batavia, Ban daung); Sumatra (Lahat); Borneo.

Specimens examined.—

Regeister No.	*Locality.*	*Donor or Collector.*	*No. of sepecimens.*
F. 108/2	King George V National Park, Kualu Tahan, Pahang, F. M. S.	Raffles Museum Singapore	1 specimen.
F. 100/2	Kuala Tahn, Pahang, F. M. S.	Do. . . .	1 specimen.
F. 110/2	Plus R. Jalong, Perak F. M. S.	Do. . . .	1 specimen.

Homaloptera ophiolepis, Bleeker.

1916. *Homaloptera ophiolepis*, Weber and Beaufort, *Fish. Indo-Austral. Archipel.*, **3**, p. 15.
1932. *Homaloptera ophiolepis*, Hora, *Mem. Ind. Mus.*, **12**, p. 287.

D. 3/8-9; A. 2/5-6; P. 4-6/9-11; V. 2/8; L. 1. 45-48.

Head 6 to 7 and depth of body 10·25 to 11·5 in total length. Head longer than broad. Diameter of eye 4·5 to 5·5 in head and 2 times in interorbital space. Snout more than half length of head. Barbels subequal and equal to or slightly longer than diameter of eye. Dorsal origin slightly ahead of pelvics. Predorsal scales 15. Abdomen scaly except the space between the pectorals. Scales on each side of the body with median keels.

Locality.—Sumatra (Lahat); Java (Parongkalong, Bandung) Borneo (Mahakam river).

Homaloptera bilineata, Blyth.

1888. *Homaloptera bilineata*, Day, *Fish. India*, **2**, p. 526, pl. cxxi, fig. 8.

1889. *Homaloptera bilineata*, Day, *Faun. Brit. India Fish.*, **1**, p. 244.

1932. *Homaloptera bilineata*, Hora. *Mem. Ind. Mus.*, **12**, p. 288, pl. x, fig. 3.

D.2/8 ; A.2/5 ; P. 4/9-10 ; V. 2/7 ; C. 19 ; L. 1.64 ; L. tr. 12/17.

Head contained 5 and depth of body 7·5 to 8 in standard length. Head much longer than broad, its width contained 1·75 in its length. Tip of snout pointed. Depth of head at occiput equal half its length. Snout more than half length of head. Eyes moderately large, diameter contained 6·5 to 6·75 in head, 3·5 in snout and 2·5 in interorbital width Interorbital space equals about length of post-orbital part of head. Mouth inferior, slightly arched and fringed by thick plain lips which are continuous at angles. Labial groove widely interrupted; barbels short, stout and equal in length. Ventral surface except between pectorals totally scaly. Scales nearly three-fourths as broad as long, with bluntly pointed apical region and broad basal portion. Dorsal commencing ahead of pelvics, and its origin closer to tip of snout than to base of caudal. Pectorals separated from pelvics by considerable distance. Least height of caudal peduncle contained 2 times in its length.

Locality :—Meetan and Tenasserim, Lower Burma.

Specimens examined.—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens. state of preservation.*
Cat. 955	....	A. S. B.	2 specimens, slightly damaged.
1226	Tenasserim, Lower Burma.	Purchased from F. Day; Original of pl. cxxi, fig. 8.	1 specimen badly desiccated.
F.11041/1	Meetan, Burma	Mus. Civ. Stor. Nat. Genova.	2 specimens.

Homaloptera orthogoniata, Vaillant.

1916. *Homaloptera orthogoniata*, Weber and Beaufort, *Fish. Indo-Aust. Archipel.*, **3**, p. 15.

1932. *Homaloptera orthogoniata*, Hora, *Mem. Ind. Mus.*, **12**, p. 288.

D. 2-3/8-9 ; A. 2-3/5-6 ; P. 5-6/10 ; V. 2/98 ; L. 1.63-67 ; L. tr. 10-1-11

Head 4·5 to 5 in standard length and 5·7 in total length. Depth of body 5 and 6·7. Diameter of eye 10 in head and 4 in interorbital space.

Scales on lateral line 63 to 67. Dorsal originates in advance to commencement of pelvics. Ventral surface except between pectorals totally scaly. Colour in alcohol brown, clouded with large distinct irregular dorsal blotches, or areas of deep brown, a large one between the dorsal and the pelvic. Ventral surface paler. A brown streak runs from side of snout to eye and is continued behind it to occiput. Another streak passes downwards across the sides of the head. All streaks with narrow pale brown margins. Fins brownish white.

This species possesses an incipient rostral groove.

Locality.—Borneo (River Raun and Bougan, System of Upper Kapuas ; Upper Mahakam river ; Baram river), Malaya Peninsula,

Specimens examined.—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F.11037/1	Howong, Borneo	Rijks Mus. Nat. Hist. Leyden.	1 specimen.
F.11038/1	Baram river, Borneo	Acad. Nat. Sci. Philadelphia.	1 specimen.
F.656/2	Perak, F. Malaya States.	Nat. Hist Mus. Stan. Univ.	1 specimen.

Homaloptera ocellata, Van der Hoeven.

1932. *Homaloptera ocellata*, Hora, *Mem. Ind. Mus.*, **12**, p. 277, pl. x, fig. 5.

D. 3/7-8 ; A. 3/5 ; P. 6-7/10-11 ; V. 2/6-7 ; L. 1.63-71.

Head 5·4 to 6 and depth of body 7·1 to 8 in total length. Diameter of eye 6·3 to 7·5 in head, 3 to 4 in snout and 2 in interorbital space. Width of head 1·4 in its length. Barbels subequal and shorter than eye. Origin of dorsal distinctly ahead of pelvics and closer to tip of snout than to base of caudal. Pelvics reach anus. Pectorals shorter than head and separated by considerable distance from pelvics. Caudal deeply forked. Abdomen scaly except a median naked portion beginning before a triangular scaly patch situated in front of pelvics.

Locality.—Jave (Batavia, Buitenzorg, Tjipauas, Tjampea, Bandung, Garut, Ngantang) ; Sumatra (Lahat).

Specimens examined.—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens and state of preservation.*
H.036/1	Java.	Rijks. Mus. Nat. Hist. Leiden.	1 specimen. Caudal fin broken.
F. 655/2	Tjiwalen Creek, Java	Univ. Mus. Zool. Minchigan, U. S. A.	2 specimens.

Homaloptera leonardi, Hora.

1941. *Homaloptera leonardi*, Hora, *Bull. Raffles Mus. Singapore*, **17**, p. 61.

D. 3/8 ; A. 2/5 ; P. 6/10-11 ; V. 2/8 ; C. 18 ; L. 1.57-60.

Head 4·3 to 4·8 in standard length and 5·3 to 6 in total length. Depth of body 8 to 9·6 and 8·7 to 12. Height of head at occiput 2 times in

its length. Diameter of eye 4·1 in head, 2 to 2·2 in snout and 1 to 1·3 in interorbital space. Least height of caudal peduncle contained 2·6 to 3 in its length.

Locality.—Malaya Peninsula (Kuala Tahang, Pahang).

Specimens examined.—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 13213/1 (Type).	Kuala Tahan, King George V National Park, Pahang, F. M. States.	Raffles Mus.	1 specimen.
F. 13214/1 (Paratypes).	Do.	Do.	7 specimens.
F. 111/2	Do.	Do.	8 specimens.

Homaloptera salusur, Bleeker.

1916. *Homaloptera erythrorhina,* Weber & Beaufort (in part), *Fish. Indo-Austral. Archip.*, **3**, p. 17.

1932. *Homaloptera salusur,* Hora, *Mem. Ind. Mus.*, **12**, p. 288.

D. 2/9-10 ; A. 2/6 ; P. 7/10-11 ; V. 2/7 ; L. 1.70-80.

Head 4·4 to 4·6 in standard length and 5·5 to over 6 in total length. Depth of body 5·8 and 7·1 to 8. Diameter of eye 6·3 to 7·5 in head, 3 to 4 in snout and more than 2 times in the interorbital width. Snout long and pointed. Pelvics extend beyond anal opening. Scales smooth, without any trace of keels.

Locality.—Java, and Sumatra.

Neohomaloptera, Herre.

1944. *Neohomaloptera,* Herre, *Proc. Biol. Soc., Washington,* **57**, p. 50.

Head and anterior part of body feebly depressed and ventral profile flattened and horizontal. Dorsal profile arched, body being deepest below commencement of dorsal. Snout broadly rounded and provided with trenchent margins. Eyes small and situated dorso-laterally. Mouth small, subterminal and slightly arched. Two pairs of rostral barbels of which inner is as long as diameter of eye. Outer barbel of maxillary angle longer than inner which is about half diameter of eye. Gill openings extend to ventral surface for a short distance. Head and body scaled, except ventral surface which is naked as far back as hind end of pelvics. Paired fins are broad and horizontal. Pectorals scarcely reach pelvics. Pectorals with 12 to 13 rays of which 3 to 4 outer rays are unbranched. Pelvics with 7 rays of which 2 outer rays are unbranched. Dorsal originates behind point of commencement of pelvic. Caudal fin rounded, its length equal or slightly less than length of head.

Genotype.—*Neohomaloptera johorensis* Herre.

Distribution.—Johore, Malaya Peninsula.

Remarks.—Herre (1944) erected the subgenus *Neohomaloptera* to accommodate a species of *Homaloptera* from Malaya Peninsula. He pointed out that from *Homaloptera* as defined by Hora (1932), *Neohomaloptera* differed in having :

"Two pairs of barbels at each angle of the mouth instead of but one ; the rays of the pectoral and ventral reduced in number, the former with 12 to 13 instead of 14 to 20 ; the latter 7 instead of 8 to 10 ; the pectorals further has but 3 to 4 simple rays instead of 4 to 8. Caudal fin slightly rounded, not forked or emarginate as in typical *Homaloptera*. Caudal peduncle is short and as deep as long."

In view of the above diagnostic characters, *Neohomaloptera* is Considered here as a distinct genus.

Neohomaloptera johorensis, Herre.

(Plate I, figs. 3 and 4.)

1944. *Homaloptera (Neohomaloptera) johorensis*, Herre, *Proc. Biol. Soc. Washington*, **57**, p. 51.

A short description of this species from a specimen I have examined, received on loan from the collection of the Stanford University, U. S. A. is given below :

D. 1/7 ; A. 1-2/5, P. 3-4/8-9 ; V. 2/5 ; L. 1. 33-35.

Head contained 3·7 to 4 and depth of body contained 5 to 5·1 in total length. Caudal contained 4 to 4·1 ; pectorals 3·6 to 4 and pelvics about 5·2 in total length. Eyes small, dorsolateral, their diameter contained 4·25 to 4·5 in head and 2 times in interorbital width. Length of snout corresponds to postorbital part of head. 2 pairs of rostral barbels, length of inner equal to diameter of eye ; outer $1\frac{1}{2}$ diameter of eye ; outer maxillary barbels longer than eye ; inner about half diameter of eye.

Body scaled, except ventral surface in front of hind end of base of pelvics. Predorsal scales 14 to 15. Caudal peduncle with 16 scales round it. Dorsal commences slightly behind origin of pelvics. Dorsal slightly shorter than head and its height contained 4·5 to 5 in total length. Pectorals about as long as head, scarcely reaching pelvics. Caudal peduncle about as long as deep.

"Colour in alcohol is more or less brown stippled with minute black specks, interspread with large circular dots. Dorsal with two transverse rows of black spots and caudal with one or two blackish crossbars. Other fins colourless" (Herre, 1944).

Locality.—Simpang Rengam, Johore, Malaya Peninsula.

Travancoria, Hora.

1941. *Travancoria*, Hora, *Rec. Ind. Mus.*, **43**, p. 228.

For the diagnostic characters of this South Indian genus reference may be made to the key for the genera on page 182. In his work on the Homalopterid fishes of Peninsular India, Hora (*loc. cit*) has given a detailed description of the genus.

Genotype.—Travancoria jonesi Hora.

Distribution.—South India (Hill ranges of Northern Travancore; Anamalai Hills, Western Ghats).

This remarkable monotypic genus was described by Hora (1941, *op. cit.*) from the Hill ranges of Northern Travancore. From *Bhavania* Hora, it is easily distinguished by its more extensive gill openings and the number of rostral barbels. *Travancoria* is also intermediate in certain characters between *Homaloptera* van Hass., and *Balitora* Gray.

Travancoria jonesi, Hora.

1941. *Travancoria jonesi*, Hora, *Rec. Ind. Mus.*, **43**, p. 230, pl. viii, fig. 5-9.
1941. *Travancoria jonesi*, Hora & Law, *Ibid.*, **43**, p. 249.
1942. *Travancoria jonesi*, Hora & Law, *J. Roy, Asiat. Soc. Bengal*, **8**, pp. 39-46.

D. 2/7-8; A. 1/4-5; P. 6/9-10; V. 2/6-7; C. 17; L. 1. 75-77.

Head 5 to 5·8 in standard and 5·9 to 6·8 in total length. Depth of body 8·33 to 8·7 in standard length and 9·87 to 10·15 in total length. Width of head contained 1 to 1·3 and height of head at occiput 1·7 to 1·9 in its length. Diameter of eye contained 4·13 to 5 in head; 2·5 to 2·6 in snout and 1·4 to 1·5 in interorbital space. Least height of caudal peduncle contained 2·25 to 2·75 in its length.

Type specimen is preserved in the collection of the Zoological Survey of India.

Locality.—South India (High Ranges, Northern Travancore; Anamalai Hills).

Specimens examined:—

Register No.	*Locality.*	*Donor or Collection.*	*No. of specimens.*
F. 13507/1 (Type)	Pampadampara, N. Travancore	S. Jones.	1 specimen.
F. 13508/1	Do.	Do.	1 specimen.
F. 13598/1	Do.	Do.	2 specimens.
F. 13599/1	Do.	Do.	1 specimen. Badly damaged; head missing.

Pseudohomaloptera gen. nov.

Small loach-like fish in which head and anterior part of body are depressed and ventral profile is flattened and horizontal. Snout broadly pointed. Eyes placed dorsolaterally, provided with free orbital margins and not visible from below. Mouth inferior, transverse, slightly arched and of moderate size. Lips are full, plain and continuous. Four rostral barbels and a pair of maxillary barbels present. Barbels equal in length and about as long as the eye. Rostral groove well developed and deep at sides of mouth. Jaws strong and provided with strong rasping edges. Gill openings oblique, extending to ventral surface for short distance.

Body covered with moderately small scales which are carinate, slightly increasing in size towards the back. Ventral surface of head and body upto anus totally scaleless. Dorsal origin before middle of length. Paired fins broad, extensive and horizontal. Pelvics not reaching anal. Pectorals reaching pelvics. Pectorals with 20 rays of which 8 outer rays are simple. Caudal fin deeply forked, the lower lobe the longer. Caudal peduncle extremely slender, its height being about three time in its length.

Genotype.—*Pseudohomaloptera tate-regani* (Popta).

Distribution.—Borneo (River Bo).

Remarks.—The genus *Pseudohomaloptera* has been erected to accommodate a previously known Bornean species described under *Homaloptera* by Popta (1905). The well defined deep rostral groove of *H. tate-regani* is of sufficient importance to give it a generic rank. Hora (1932, p. 327) commented on the peculiar rostral groove of this species, but at that time he did not separate it into a new genus. In view of a thorough revision of the species of *Homaloptera*, it was found difficult to retain it in that genus on account of the presence of a rostral groove and other structures associated with the mouth.

Pseudohomaloptera tate-regani (Popta).

1905. *Homaloptera tate-regani*, Popta, *Notes Leyden Mus.*, **25**, p. 180.

1906. *Homaloptera tate-regani*, Popta, *Ibid.*, **27**, p. 182.

1916. *Homaloptera tate-regani*, Weber & Beaufort, *Fish. Ind. Austral. Archip.*, **3**, p. 19.

1932. *Homaloptera tate-regani*, Hora, *Mem. Ind. Mus.*, **12**, p. 288, pl. xi, fig. **4**.

D. 3/8 ; A. 2/5 ; P. 8/12; V. 2/8 ; L. 1. 64 ; L. tr. 6/1/7.

Head 4·5 in standard and 6 in total length. Depth of body 7·45 and 10 ; Diameter of eye 7 in head ; 4 in snout and 3 in interorbital width. Origin of dorsal ahead of pelvics. Ventral surface upto vent totally scaleless. Least height of caudal peduncle contained more than three, times in its length.

For detailed diagnosis of this species reference may be made to the description of the genus.

Locality.—Borneo (River Bo).

Balitora Gray.

1941. *Balitora*, Hora, *Rec. Ind. Mus.*, **43**, p. 222.

1945. *Balitora*, Smith, *Bull. U. S. Nat. Mus.*, **188**, p. 278.

1948. *Balitora*, Ramaswami, *Proc. Zool. Soc. London*, **118**, p. 513.

For the diagnostic characters of *Balitora* reference may be made to the key for the genera on page 182. Hora (1941) has redefined the genus.

Genotype.—*Balitora brucei* Gray.

Distribution.—South India (Mysore) ; Northern India (Bhutan, Northern Bengal ; Sishak river, Chittagong Hills) ; Burma (Meekalan ; Pegu ; Sankha stream, Kamaing, Myitkyina District).

Key to the species of the genus Balitora *Gray.*

I. Pectorals missing or just reaching pelvics ; lower caudal lobe considerably longer than upper . . . . *B. brucei.*

II. Pectorals extending beyond commencement of pelvics ; lobes of caudal almost equal in length . . . . *B. maculata.*

Balitora brucei Gray.

1832. *Balitora brucei*, Gray, *Ill. Ind. Zool.*, **1**, pl. lxxxviii, fig. 1.

1920. *Balitora brucei*, Hora, *Rec. Ind. Mus.*, **19**, p. 197.

1932. *Balitora brucei*, Hora, *Mem. Ind. Mus.*, **12**, p. 291, pl. x, fig. 1, pl. xi, fig. 5 ; pl. xii, fig. 2.

D. 3/8 ; A. 2/5 ; P. 10/11-12 ; V. 2/9 ; C. 17 ; Ll. 70 ; L. tr. 10/7.

Head contained 6·5 and depth of body about 11 to 13·5 times in total length. Head slightly longer than broad, its width contained about 0·8 in its length. Diameter of eye contained 6·6 in head, 3·6 in snout and about 2·7 in interorbital space. Snout broad and trenchent. Least depth of caudal peduncle contained about three times in its length.

This type and well known species of the genus *Balitora* is represented in the collection of the Zoological Survey of India, Indian Museum, by a fine series of specimens obtained from Darjeeling and the Khasi Hills in Assam.

Specimens examined :—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
1509	Darjeeling.	Purchased from F. Day.	1 specimen. Bad state of preservation.
F. 9857-9/1	Cherrapunji, Assam	Bourne.	3 specimens. Partly damaged.
F. 10239/1	Tang-Siang stream Cherrapunji, Assam.	S. L. Hora .	8 specimens.
F. 11092/1	Non-priang stream below Cherrapunji, Assam.	Do.	3 specimens.
F. 685/2	Right bank of Kauala river, N. E. of Jainagur Railway stn., Darbhanga Dt., Bihar.	Do.	2 specimens.

Three geographical races of *Balitora brucei* are recognised at present. They are *B. brucei mysorensis* Hora in Mysore, South India ; *B. brucei burmanicus* Hora in Burma and *B. brucei melanosoma* Hora on the Burma-Siam border. These are dealt with below.

Balitora brucei var. mysorensis Hora.

1941. *Balitora brucei* var. *mysorensis*, Hora, *Rec. Ind. Mus.*, 43, p. 232, pl. viii, fig. 4.

D. 3/9 ; A. 2/5 ; P. 9/12 ; V. 2/9 ; C. 19 ; L. 1.68.

Head contained 4·3 in standard and 5·64 in total length. Depth of body contained 7·6 and 9·8 width of head contained 1·41 and height of head at occiput 2·23 in its length. Diameter of eye 5·56 in head; 3·44 in snout and 1·81 in interorbital space. Snout more or less pointed. Least height of caudal peduncle contained 3 times in its length.

Locality.—South India (Sivasamudram, Mysore State).

In addition to the type preserved in the collection of the Zoological Survey of India, I have recently examined a few more specimens of this variety, of which one is deposited in the collection.

Specimens examined :—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 13512/1	Sivasamudram, alt. 1500—2000 ft., Mysore State, S. India.	B. S. Bhimachar.	1 specimen.
F. 686/2	Mysore.	E. G. Silas	1 specimen.

Balitora brucei var. **burmanicus** Hora.

1932. *Balitora brucei* var. *burmanicus*, Hora, *Mem. Ind. Mus.*, **12**, p. 291.

This variety of *B. brucei* differs from the *forma typica* in having a more narrower body, more elongate head and darker colouration. It is represented in the collection of the Zoological Survey of India by a good series of specimens.

Specimens examined :—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 11034/1 (Type).	Meekalan, Burma	Genova Museum.	3 specimens.
F. 10284/90	Pegu, Burma	N. Theobald	6 specimens.
F. 11042/1	Shishak river, Chittagong Hills.	R. P. Mullon	4 specimens.
F. 10886/1	Sankha stream, Kamaing and Mogaling, Myitkyina District, N. Burma.	B. N. Chopra.	1 specimen.
F. 656/2	Mooleyit, Burma	U. S. Nat. Mus.	1 specimen.

Balitora brucei var. **melanosoma** Hora.

1932. *Balitora brucei* var. *melanosoma*, Hora, *Mem. Ind. Mus.*, 12, p. 291.

For a specimen of *Balitora brucei* (No. 1920., 9. 8. 11) in the collection of the British Museum, Hora (*op. cit.*), gave a subspecific rank and designated it as *melanosoma*. Intermediate between the *forma typica* and the Burmese race, *B. brucei burmanicus*, it is a melanic variety in which the dorsal surface, except the tips of the fins, are dirty white in colour.

Locality.—Lower Burma (Thaungyiu River, (Megla stream) on the Burma-Siam border).

Balitora maculata Gray.

1920. *Balitora maculata*, Hora, *Rec. Ind. Mus.*, **19**, p. 199, fig. 2., pl. xi, fig. 1.
1932. *Balitora maculata*, Hora, *Mem. Ind. Mus.*, **12**, p. 291.

D. 2/9 ; A. 2/5 ; P. 19 ; V. 2/7 ; C. 17 ; L. 1. 70.

Head contained 5·5 and depth of body 9·5 to 10 in standard length. Diameter of eye contained 8 in head, 4 to 4·2 in snout. Head about as long as broad. Snout broadly rounded. Pectorals overlap pelvics.

Specimens examined :—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 9860-651/1	Darjeeling	N. Wallich	2 specimens . (in bad state of preservation).

Balitoropsis Smith.

1945. *Balitoropsis*, Smith *Bull. U. S. Nat. Mus.*, **188**, p. 278.

Body more or less cylindrical ; anteriorly slightly depressed. Head greatly depressed and obtusely pointed ; abdomen and under surface of head flattened. Depth of body and width at origin of dorsal about equal. Mouth small, moderately arched and subterminal. A deep narrow groove extending around the corners of mouth. Well developed rostral barbels in two closely approximated groups, occupying a median rostral lobe ; nostrils large, separated by a flap. Lips finely papillated, upper lip covering upper jaw, lower lip leaving the sharp edged of lower jaw exposed. Scales on back and sides carinated. Head and anterior part of abdomen scaleless. Gill openings oblique, extending to ventral surface for short distance. Vent situated much nearer pelvic base than origin of anal fin. Dorsal arising in advance of pelvics. Pectorals with 14 rays of which 4 rays are simple. Pectorals separated from pelvics by a considerable distance. Pelvics extend far beyond anal opening, but fall short of anal fin. Pelvics with 10 rays of which 2 outer rays are simple. Top and sides of head thickly covered with papillae which are absent on the ventral surface.

Genotype.—*Balitoropsis bartschi* Smith.

Distribution.—Peninsular Siam (Kao Chang, Trang Province).

Balitoropsis bartschi Smith.

1945. *Balitoropsis bartschi*, Smith, *Bull. U. S. Nat. Mus.*, **188**, p. 279, fig. 56.

D. 2/7 ; A. 2/5 ; P. 4/10 ; V. 2/8 ; L. 1. 44 ; L. tr. 7/1/6.

Head 4·4 in standard length ; depth of body equals length of head. Diameter of eye 5 in head, 2·5 in snout and 2 in interorbital space. Eyes situated in posterior half of head. Scales in predorsal region 13. Least depth of caudal peduncle contained 1·8 in its length. For detailed diagnosis reference may be made to the description of the genus.

Locality.—Stream on Kao Chong in Trang Province, Peninsular Siam.

Sinohomaloptera Fang.

1932. *Sinohomaloptera*, Hora, *Mem. Ind. Mus.*, **12**, p. 288.
1938. *Sinohomaloptera*, Herre, *Lingnan Sci., Journ., Canton*, **17**, p. 429.
1943. *Homaloptera*, Nichols, *Nat. Hist. Cent. Asia*, **9**, p. 220.
1949. *Sinohomaloptera*, Chen & Liang, *Quart. Journ., Taiwan Mus.*, **2**, (4). p. 161.

For the diagnostic characters of *Sinohomaloptera* reference may be made to the key for the genera on page 182. For a detailed description of the genus, Hora (*loc. cit.*) may be consulted.

Genotype.—*Sinohomaloptera kwangsiensis* Fang.

Distribution.—Cheng Kon Tsuen, Hainan ; Kwangsi ; China.

Remarks.—Fang (1930, *vide supra*, p. 187) distinguished *Sinohomaloptera* from *Homaloptera* on the nature of the basipterygium and the modified ribs. Herre (1938) described a new species, *S. hoffmanni* from Hainan in China. In the possession of a pair of barbels at each angle of the mouth *Sinohomaloptera* shows affinities to the Malayan genus *Neohomaloptera*. But the rostral fold, papillate lips and larger number of rays in the paired fins distinguishes it from *Neohomaloptera*.

Key to the species of the genus Sinohomaloptera *Fang.*

I. Pectorals 7/11 ; scales on lateral line 61 to 64 ; snout less than two times in head ; pelvics extending beyond anal opening for a short distance . . *S. hoffmanni.*

II. Pectorals 8/12 ; scales on lateral line 66 ; snout more than two times in head ; pelvics do not reach anal opening *S. kwangsiensis.*

Sinohomaloptera hoffamanni Herre.

1938. *Sinohomaloptera hoffmanni*, Herre, *Lingnan Sci, Journ.*, **17**, p. 429, fig. 1.
1943. *Homaloptera (Octonema) hoffmanni*, Nichols, *Nat. Hist. Cent. Asia*, **9**, p. 221.

D. 3/7 ; A. 2/5 ; P. 7/11 ; V. 2/8 ; L. 1. 61-64.

Head 4·4 to 4·5 and depth of body 6·9 to 7·1 in total length. Diameter of eye 5·8 in head and 3·2 in snout. Length of snout is 1·8 in head Interorbital space twice diameter of eye. Least depth of caudal peduncle contained 2·25 in its length. Dorsal originates ahead of pelvics and is situated closer to tip of snout than to base of caudal.

Locality.—Cheung Kon Tsuen, Hainan, China.

Sinohomaloptera kwangsiensis Fang.

1930. *Homaloptera (Sinohomaloptera) kwangsiensis*, Fang, *Sinensia*, **1**, (3), p. 27
1930. *Sinohomaloptera kwangsiensis*, Fang, *Contr. Biol. Lab. Sci. Soc. Canton. (Zool, Ser.)*, **6**, p. 26.
1932. *Sinohomaloptera kwangsiensis*, Hora, *Mem. Ind. Mus.*, **12**, p. 289.
1943. *Homaloptera (Sinohomaloptera) Kwangsiensis*, Nichols, *Nat. Hist. Cent Asia*, **9**, p. 222.
1949. *Sinohomaloptera kwangsiensis*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 161.

D. 2/8 ; A. 2/5 ; P. 8/12, V. 2/8 ; L. 1.66.

Head contained 4·73 and width of body 5·74 in standard length. Head longer than broad, and its width contained 1·41 in its length. Snout slightly less than half length of head. Interorbital width contained 2·83 in head. Eyes moderately large, its diameter contained 5·5 in head. Origin of dorsal slightly ahead of pelvics, and nearer tip of snout than to base of caudal.

Locality.—Kwangsi China.

Specimens examined :—

Register No.	*Locality.*	*Donor or collector.*	*No. of specimens.*
F. 11111/1	Kwangsi, China	Met. Mus. Nat. Hist. Nanking.	1 specimen.

Lepturichthys Regan.

1932. *Lepturichthys*, Hora, *Mem. Ind. Mus.*, **12**, p. 29.
1933. *Lepturichthys*, Fang, *Sinensia*, **4**, (3), p. 48.
1943. *Lepturichthys*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 222.
1949. *Lepturichthys*, Chon & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 162.

For the diagnostic characters of *Lepturichthys* reference may be made to the key for the genera on page 182. The genus was redefined by Hora in (1932).

Genotype.—*Lepturichthys fimbriata* (Günther).

Distribution.—Upper Yangtse Kiang River ; Min river ; Szechuan, Ichang, Hupeh Province ; Tungtin Lake, Hunan Province ; China.

Remarks.—Regan (1911), created the genus *Lepturichthy* for Günther's species *Homaloptera fimbriata*, and in briefly defining it brought out its differences from that of *Homaloptera*. Later Nichols (1928) assigned several specimens collected from Tungting Lake to *L. fimbriata* (Günther). Hora (1932) differentiated the known specimens of *L. fimbriata* into three species, and defined the genus *Lepturichthys* as : "Tail long and slender, least height of caudal peduncle less than diameter of eye ; fimbriated lips ; three barbels at each angle of the mouth." For the interrelationships of *Lepturichthys* with the other Chinese Homalopteriadae reference may be made to the discussion on page 247.

Key to the species of the genus Lepturichthys *Regan.*

I. Greater part of dorsal surface of head and body smooth ; low keels on scales in tail region and some keels on scales on anterior part of body provided with spinous projections at their ends.

  A. Seven anterior simple rays in the pectoral ; longest ray of dorsal shorter than head . . *L. fimbriata.*

  B. Nine anterior simple rays in pectoral ; longest ray of dorsal much longer than head . . *L. güntheri.*

II. Entire dorsal surface of head and body covered with wart-like spinous processes ; large scales in front of dorsal with 3 or 4 warts on their distal borders *L. nicholsi.*

Lepturichthys fimbriata (Günther).

1932. *Lepturichthys fimbriata*, Hora, *Mem. Ind. Mus.*, **12**, p. 294.
1933. *Lepturichthys fimbriata*, Fang, *Sinensia*, **4**, (3), p. 49.
1943. *Lepturichthys fimbriata*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 220-233.
1949. *Lepturichthys fimbriata*, Chen & Liang, *Quart. Journ., Taiwan Mus.*, **2**, p. 162.

D. 3/8 ; A. 2/5 ; P. 7/11-12 ; V. 3/8.

Head contained 6·3 in standard and 7·2 in total length. Depth of body contained 12·6 in standard and 14·5 in total length. Height at occiput half width of head, which in turn is contained 1·1 times in length of head. Diameter of eye contained 6·4 in head, 3·7 in snout and 2·5 in interorbital space. Length of caudal peduncle contained 3·8 in standard length. Least depth of caudal peduncle contained 16 times in its length.

Locality.—Ichang ; Hupen Province, China.

Lepturichthys güntheri Hora.

1932. *Lepturichthys güntheri*, Hora, *Mem. Ind. Mus.*, **12**, p. 295.
1933. *Lepturichthys güntheri*, Fang, *Sinensia*, **4**, (3), p. 49.
1943. *Lepturichthys güntheri*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 225.
1949. *Lepturichthys güntheri*, Chen & Liang, *Quart. Journ. Taiwan Mus* ,*2*. p. 162.

D. 3/8 ; A. 2/5 ; P. 9/11-12 ; V. 3/9.

Head contained 6·2 to 6·9 and depth of body 11 to 11·5 in standard length. Width of head contained 1·2 times and height at occiput 2 to 2·2 in its length. Diameter of eye contained 6·6 to 7·7 in head, 4 to 4·5 in snout and 2·8 to 3 in interorbital space. Length of caudal peduncle contained 2·9 to 3·2 in standard length. Its least height contained 19 to 23 times in its length.

Locality.—Min River, Szechuan, China.

Lepturichthys nicholsi Hora.

1932. *Lepturichthys nicholsi*, Hora, *Mem. Ind. Mus.*, **12**, p. 297.
1933. *Lepturichthys nicholsi*, Myers, *Copia*, **2**, p. 109.
1933. *Lepturichthys nicholsi*, Fang, *Sinensia*, **4**, (3), p. 50.
1943. *Lepturichthys nicholsi*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 225.
1949. *Lepturichthys nicholsi*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 162.
1950. *Lepthurichthys nicholsi*, Hora, *Rec. Ind. Mus.*, **48**, p. 52.

D. 3/8 ; A. 2/5 ; P. 7-8/11 ; V. 3/7.

Head contained 5·9 to 6·1 and depth of body 10 tc 11 in standard length. Width of head contained 1·2 and height at occiput 2·1 to 2·2 in its length. Diameter of eye contained 6·1 to 6·3 in head, 3·3 to 3·5 in snout and 2·4 in interorbital space. Length of caudal peduncle contained 3·3 to 3·4 in standard length. Least height of caudal peduncle contained 17 to 18 times in its length.

Locality.—Tungting Lake, Hunan, China.

Specimens examined :—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 11093/1	Tungting Lake, Hunan, China.	Amer. Mus. Nat. Hist.	1 specimen. Caudal and pectoral on one side damaged.
F. 668/2	Do.	Do.	2 specimens.

Remarks.—*L. nicholsi* is readily distinguished from *L. fimbriata* and *L. güntheri*, by the rugose condition of the entire dorsal surface. Myers (1933) threw doubts on the validity of *L. nicholsi* and stated that the wart-like "processes may be nothing more than nuptial tubercles". Hora (1950), after an examination of a number of specimens of *L. nicholsi* in the collection of the American Museum of Natural History has confirmed his earlier findings, *viz.*, that *L. nicholsi* is a distinct species.

The type-specimen of *L. nicholsi* (F. 11098/1), preserved in the collection of the Zoological Survey of India, seems to have been lost, most probably in the floods of the Varuna River at Banaras in September 1943. All the present specimens are, however, paratypes.

Hemimyzon Regan.

1932. *Hemimyzon*, Hora, *Mem. Ind. Mus.*, **12**, p. 298.
1949. *Hemimyzon*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 162.

For the diagnostic characters of *Hemimyzon* reference may be made to the key for the genera on page 183. The genus was redefined by Hora in 1932.

Genotype.—*Hemimyzon formosanum* (Boulenger).

Distribution.—China (Yao-tan, Luchow; Leang-Chang-Shien in Szechuan; Min river, Szechuan; Taiko river in central Formosa).

Remarks.—The genus was erected by Regan (1911) to accommodate Boulenger's *Homaloptera formosanum* from Formosa. Since then 4 more species from China have been added to this genus. Fang (1930) and Hora (1931) included *Psilorhynchus sinensis* Sauvage & Dabry (1874), under *Hemimyzon*. Hora (1931) assigned *Homaloptera abbreviata* Günther to this genus. Later in 1932 he showed that Fang's species *Sinohomaloptera yaotanensis* and *S. acuticauda*, rightly belonged to *Hemimyzon*. Since then no new additions have been made to the genus.

Key to the species of the genus Hemimyzon *Regan.*

1. Pectorals with 20 to 21 rays and pelvics with 12 rays—
   - A. Scales spinous; caudal lobes roundish; L.1·71 . *H. yaotanensis.*
   - B. Scales smooth; caudal lobes pointed; L.1·72 . . *H. acuticauda.*

II. Pectorals with 22 to 26 rays and pelvics with 15 to 18 rays—

A. Scales smooth ; anterior nostril in a short tubule ; Pectorals extending beyond origin of pelvics.

1. Caudal much longer than head ; D. 3/8 ; A. 2/5 ; L. 1·75. .. .. *H. abbreviata*

2. Caudal as long as head ; D. 2/7 ; A. 1/5 ; L. 1·70 . *H. formosanum.*

B. Scales keeled ; anterior nostril with two flaps, the secondary minute ; pectorals just reaching origin of pelvics. .. .. *H. sinensis.*

Hemimyzon yaotanensis (Fang).

1949. *Hemimyzon yaotanensis*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, p. 161.

D. 2/8 ; A. 2/5 ; P. 8/12 ; V. 4/8 ; L. 1.71.

Head contained 4·81 and depth of body 7·53 in standard length. Width of head in its length 1·41 ; diameter of eye 6·25 in head. Snout 1·79 and interorbital space 2·72 in head. Depth of caudal peduncle 2·4 in head ; its length 1·34. Width of mouth 2·14 in snout.

Locality.—China (Yao-tan, Wachang ; Luchow, Szechuan).

Hemimyzon acuticauda (Fang).

1931. *Sinohmaloptera yaotanensis acuticauda*, Fang, *Sinensia*, **I**, (9), p. 143.

1949. *Hemimyzon acuticauda* Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 161.

D. 2/8 ; A. 2/5 ; P. 8/12 ; V. 4/8 ; L.1.72.

Head contained 4·69 and depth of body 7·57 in standard length. Width of head in its length 1·12. Diameter of eye in head 5·65. Snout in head 1·74 and interorbital width 2·82. Depth of caudal peduncle 2·75 and its length 1·57 in head. Width of mouth 2·32 in snout.

Locality.—China (Yao-tan, Wa-chang, Luchow, Szechuan).

Hemimyzon abbreviata (Günther).

1932. *Hemimyzon abbreviata*, Hora, *Mem. Ind. Mus.*, **12**, p. 301.

1949. *Hemimyzon abbreviata*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, p. 161.

D. 3/8 ; A. 2/5 ; P. 12/12 ; V. 3/12 ; L. 1.75.

Head contained 5·3 to 5·5 in standard and 6·8 to 7·2 in total length. Depth of body 7·5 in standard length. Head little over twice its height at occiput and 1·4 times its width in front of base of pectoral. Snout considerably more than half length of head. Diameter of eye contained 6·5 in head ; 4 in snout and nearly 3 in interorbital width. Gape of mouth contained slightly over two times in width of head and 3 in its length. Origin of dorsal behind that of pelvics, but much nearer tip of snout than to base of caudal. Pectorals reach base of pelvics. Pelvics separated from anal opening by a short distance. Caudal peduncle long and narrow, its least height contained 4·3 to 4·5 in its length.

Locality.—China (Min river Drainage, Szechuan).

Hemimyzon formosanum (Boulenger).

1919. *Hemimyzon formosanum*, Oshima, *Ann. Carnegie Mus.*, **12**, p. 196.
1932. *Hemimyzon formosanum*, Hora, *Mem. Ind. Mus.*, **12**, p. 299.
1949. *Hemimyzon formosanum*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 162.

D. 2/7 ; A. 1/5 ; P. 22(11/11) ; V. 15-16 ; L. 1.70.

Head contained 5 times and depth of body 7 times in total length. Diameter of eye contained 6 in head and 3 in snout. Interorbital width 2·33 in length of head. A pair of barbels at each angle of the mouth. Scales smooth. Pectorals overlap pelvics.

Locality.—Formosa (Taiko river).

Specimens examined :—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F.666/2	Karoton, Formosa.	Am. Mus. Nat. Hist.	2 specimens.

Hemimyzon sinensis (Sauvage & Dabry).

1930. *Hemimyzon sinensis*, Fang, *Contr. Biol. Lab. Sci. Soc. China*, **6**, (4), p. 30.
1932. *Hemimyzon sinensis*, Hora, *Mem. Ind. Mus.*, **12**, p. 299.
1949. *Hemimyzon sinensis*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 161.

D. 3/9 ; A. 1/6 ; P. 12/14 ; V. 4/14 ; L. 1.69.

Head contained 5·10 and depth of body 8·3 in standard length. Width of head in its length 1·37. Diameter of eye in head 10. Snout in head 2·66 and interorbital space 2·94. Depth of caudal peduncle 2·55 in head, and its length 0·80. Width of mouth about equal to length of snout.

Locality.—China (Loochow, Szechuan).

Sinogastromyzon Fang.

1931. *Sinogastromyzon*, Fang, *Sinensia*, **2**, (3), p. 48.
1932. *Sinogastromyzon*, Hora, *Mem. Ind. Mus.*, **12**, p. 302.
1935. *Sinogastromyzon*, Pellegrin & Fang, *Bull. Soc. Zol.*, **40**, p. 232.
1944. *Sinogastromyzon*, Chang, *Sinensia*, **15**, p. 53.
1949. *Sinogastromyzon*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 162.

The diagnostic features of *Sinogastromyzon* are given in the key to the genera on page 182. For a detailed description reference may be made to Fang (1931) and Hora 1932.

Genotype.—*Sinogastromyzon wui* (Fang).

Distribution.—China (San-fang, Lo-Ching-shien and Tung-kwei, Lung-chow, Kwangsi ; Hsia-shih, Ma-ha-hsien, Kweichow ; Anning river near Taihoechang ; Sichang ; Szechuan ; San-ho-shien, South Kwei-chow) ; Indo-China (Tonkin).

Remarks.—The genus is at present known from seven species distributed in Central and Southern China and Indo-China. *Sinogastromyzon* superficially resembles *Gastromyzon* of the family *Gastromyzonidae*. Hora (1932) recognised two species of *Sinogastromyzon*, *viz.*, *S. wui* Fang and *S. szechuanensis* Fang. Fang (1930) described *S. hsiashiensis*, *S. sanhoensis* and *S. intermedius*, all from China. Pellegrin and Chevey (1935) reported a new species, *S. tonkinensis* from Indo-China. In 1944 Chang described *S. sichangensis* from Sichang Province, China.

Key to the species of the genus Sinogastromyzon *Fang.*

I. Pelvic fin with a well developed muscular base; upper surface of poctoral and pelvic base and part above and below pelvic origin scaleless; scales without dermal ridges; anal with two anterior simple rays or with a spine consisting of two coalacent (spine is separable into two rays) anterior simple rays—

A. Lateral line scales 52 to 64—

1. Anal with two simple rays; sides of body covered by free portion of pectoral partly scaly; scales keeled. L. 1·64. .. .. .. *S. szechuanensis.*

2. Anal with a spine consisting of two coalacent anterior simple rays; sides of body covered by free portion of pectorals entirely scaleless. Scales not keeled.

a. L. 1. 52; P. 12/15; V. 8/15; L. tr. 9½/7 *S. tonkinensis.*

b. L. 1. 57-61; P. 12/13; V. 7/11/3; L. tr. 10½/2½. .. .. *S. hsiashiensis.*

B. Lateral line scales 73-75 .. .. *S. sichangensis.*

II. Pelvic fin without or with only slightly marked muscular base. Pectoral and pelvic base and part above and before pelvic origin scaly; scales more or less with dermal ridges; anal with a strong laterally grooved spine consisting of two coalacent anterior simple rays—

A. Sides of body before pelvic origin partly scaly—

1. Scaleless portion restricted to anterior ⅓ the length from the pectoral axil to the pelvic origin; anal spine smooth at its posterior edge; L. 1. 61-63. .. .. *S. wui.*

2. Sealeless portion restricted to ½ or more the length from the pectoral axil to the pelvic origin. Anal spine finely serrated at its posterior edge. L. 1. 53-58. .. .. .. *S. sanhoensis.*

B. Sides of body before pelvic origin scaleless (and below the line drawn from the pelvic origin to posterior insertion of pectoral scaleless entirely. Anal spine finely serrated at its posterior edge. L. 1. 61). .. .. *S. intermedius.*

Sinogastromyzon szechuanensis Fang.

1943. *Sinogastromyzon szechuanensis*, Nichols, *Nat. Hist. Central Asia*, 9, p. 233.

1949. *Sinogastromyzon szechuanensis*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, 2, (4), p. 163.

D. 2/8 ; A. 2/5 ; P. 12/13 ; V. 21(6-8/13-14) ; L.1· 64 ; Ltr. 11/9½.

Head contained 4·8 and depth of body 7·42 in standard length. Head about as long as broad. Diameter of eye 5·8 in head. Snout 1·8 and interorbital space 2·6 in head. Least depth of caudal peduncle 2·6 and its length 1·7 in length of head. Width of mouth in snout 1·4.

Locality.—China (Szechuan).

I have examined a specimen of this species, recently received on loan from the university of Michigan, Ann Abor, U.S.A.

Sinogastromyzon tonkinensis Pellegrin & Chevey.

1935. *Sinogastromyzon tonkinensis*, Pellegrin & Chevey, *Bull. Soc. Zool.* **40,** p. 232, fig. 1.

D. 2/8 ; A. 1/5 ; P. 12/15 ; V. 8/15 ; L. 1·52 ; L. tr. 9½/7.

Head contained 5 in standard and 6 in total length. Depth of body contained 6·2 in standard and 7·5 in total length. Head considerably broader than long. Snout broad, with trenchent margins ; its length about 1·5 in head. Diameter of eye about 5·5 in head ; 3·5 in snout and about 3 in interorbital width. Least depth of caudal peduncle 1·75 in its length. Depth of caudal peduncle in head about 3·2 and its length about 1·5.

Locality.—Indo-China (Lai Ahau ; Tonkin).

Sinogastromyzon hsiashiensis Fang.

1931. *Sinogastromyzon hsiashiensis*, Fang, *Sinensia*, **2,** (3), p. 48, fig. 3-5.

D. 2/8 ; A. 1/5/1 ; P. 12/13 ; V. 7/11/3 ; L. 1.57-61 ; L. tr. 10½/2½.

Head contained 4·5 and depth of body 5·9 to 6 in standard length. Head broader than long and its width contained 0·95 in its length. Diameter of eye in head 5·4. Snout 1·52 and interorbital width 2·34 in head. Depth of caudal peduncle 2·9 in head and its length 1·96. Width of mouth 1·44 in snout.

Locality.—China (Hsia-shih, Ma-ha-asien, Kweichow).

Sinogastromyzon sichangensis Chang.

1944. *Sinogastromyzon sichangensis*, Chang, *Sinensia*, **15,** p. 63.

D. 2/8 ; A. 2/5 ; P. 11-12/12-13 ; V. 6-7/8-11 ; L. 1·73-75 ; L. tr. 12/9.

Head contained 4·7-4·8 and depth of body 5 to 6·3 in standard length. Head much broader than long and its width equal 0·8 to 0·9 in its length. Snout 1·8 to 1·9 and interorbital space 2 to 2·4 in head. Origin of dorsal much nearer to tip of snout than to base of caudal. Anal with two anterior simple rays. The much larger number of scales in the lateral line distinguishes this species from the other members of the genus.

Locality.—China (Anning River, Tai Hochang, Sichang).

Sinogastromyzon wui Fang.

1930. *Sinogastromyzon wui*, Fang, *Sinensia*, **1**, (3), p. 36.
1931. *Sinogastromyzon wui*, Fang, *Sinensia*, **2**, (3), p. 53.
1932. *Sinogastromyzon wui*, Hora, *Mem. Ind. Mus.*, **12**, p. 303.

D. 2/8 ; A. 1/5 ; P. 12/10-16 ; V. 8/15 ; L.1.61-63.

Head contained 4·3 and depth of body 6·1 in standard length. Head about as long as broad. Diameter of eye in head 4·8. Snout in head 2·1 and interorbital width 2·41. Depth of caudal peduncle in head 2·1 and its length 2·3 ; width of mouth 1·5 in snout.

Locality.—China (San-fang, Lo-ching-shien ; and Tung-Kwei, Lung-Chow in Kwangsi).

Sinogatromyzon sanhoensis Fang.

1931. *Sinogastromyzon sanhoensis*, Fang, *Sinensia*, **2**, (3), p. 56, fig. 9.
1943. *Sinogastromyzon sanhoensis*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 233.
1949. *Sinogastromyzon sanhoensis*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 163.

D. 2/8 ; A. 1/5 ; P. 14/15 ; V. 8/12 ; L. 1.53-58 ; L. tr. $8\frac{1}{2}/8\frac{1}{2}$-9.

Head 4·9 and depth of body 6·4 in standard length. Width of head in its length 1·16. Diameter of eye 5·65. Snout in head 1·68 and interorbital width 3·3. Depth of caudal peduncle in head 2·91 and its length 1·46. Width of mouth in snout 2·1.

Locality.—China (San-ho-shien, South Kweichow).

Specimens examined :—

Register No.	*Locality.*	*Donor or collector.*	*No. of specimens.*
F. 667/2			1 specimen.

Sinogastromyzon intermedius Fang.

1930. *Sinogastromyzon wui*, Fang (in part), *Sinensia*, **1**, (3), pp. 36-41.
1931. *Sinogastromyzon intermedius*, Fang, *Sinensia*, **2**, (3) pp. 54-56.

D. 2/8 ; A. 1/4/1 ; P. 12-13/12-13 ; V. 8/12/1 ; L. 1·61 ; L. tr. $8\frac{1}{2}/8\frac{1}{2}$.

Head contained 3·75 and depth of body 6 in standard length. Head about as long as broad. Diameter of eye 5·92 in head. Snout 2·3 in head and interorbital width 2·96. Depth of caudal peduncle 2·55 in head and its length 1·85. Width of mouth 1·5 in snout.

Locality.—China (Tung-Kwei, Lung-Chow, South Western Kwangsi).

Metahomaloptera Chang.

1944. *Metahomaloptera*, Chang, *Sinensia*, **16**, p. 54.

A short description of the genus *Metahomaloptera* after Chang (*loc. cit.*), is given below :

Head and anterior part of body greatly depressed, while tail region is compressed from side to side. Ventral profile in front of pelvics flattened and horizontal. Snout broadly pointed. Mouth small, inferior, cresent shaped and less than one third in width of head. Upper lip narrow,

possessing a single row of papillae ; lower lip plain and thin. Both jaws provided with sharp horny edges. 8 minute barbels, 4 rostral and 4 maxillary. Gill-openings small, cresent shaped and restricted to considerably above base of pectoral fin. Width of gill opening about twice diameter of eye. Body covered with small cycloid scales. Lateral line straight and complete with 70 to 75 scales along it. Dorsal originates midway between tip of snout and base of caudal or slightly nearer the latter. Pectoral overlaps pelvics and possesses 20 to 23 rays of which 9 to 11 are simple. Pelvics completely united posteriorly to form a suctorial disc ; its origin slightly ahead of that of dorsal. Pelvics with 17 to 21 rays of which anterior 5 to 8 are simple, middle 7 to 12 branched and posterior 2 to 4 simple. A muscular band present above pelvic base. Anal reaches caudal which is slightly emarginate and is about as long as head. Vent situated immediately in front of anal fin.

Genotype.—Metahomaloptera omeiensis Chang.

Distribution.—China (Loshan and Omei).

Remarks.—This monotypic genus, like *Bhavania* of South India, is remarkable among the Homalopteridae in possessing very small gill-openings, a condition which is also seen in several genera of the family Gastromyzonidae. The United pelvics and the greatly restricted gill-openings give *Metahomaloptera*, a place in the Homalopteridae similar to that of *Gastromyzon* among the Gastromyzonidae.

Metahomaloptera omeiensis Chang.

1944. *Metahomaloptera omeiensis*, Chang, *Sinensia*, **16**, p. 54.

D. 2/7-9 ; A. 2/5 ; P. 20-23(9-10/10-13) ; V. 17-21(5-8/7-12/2-4) ; L.1·70-75.

Head 4·6 to 5·1 and depth of body 4·4 to 6·2 in standard length. Depth of head in its length 1·5 to 1·8 ; width of head 0·7 to 0·8. Diameter of eye 4·6 to 5·5. Snout in head 1·6 to 2 and interorbital space 1·7 to 2. Least depth of caudal peduncle 2·7 to 3 in head and its length 1·9 to 2·5. Origin of dorsal equidistant from tip of snout and base of caudal.

Locality.—China (Loshan and Omei).

VI.—DOUBTFUL HOMALOPTERIDAE.

? **Juvenile Homalopterid.**

? *juvenile Homalopterid*, Silas, *J. Zool. Soc. India*, **3**, (1), p. 14, fig 1.

A peculiar Homalopterid was recently described (Silas, 1951) from Borneo. This form is characterized by the following important features :

D. 3/7 ; A. 1/4 ; P. 7/14 ; V. 5/11 ; C. 17.

Snout broadly rounded ; Lips thin, non-papillated, continuous at angles of mouth. Four rostral barbels ; a pair of barbels at each corner of the mouth. Gill-openings extend to opposite base of pectoral fin. Dorsal commences in advance to pelvics and is placed nearer base of

caudal than to tip of snout. Pectoral reaches pelvic base. Pelvics free from each other and not uniting to form a disclike structure.

For detailed diagnosis reference may be made to Silas (*op. cit.*).

Locality.—Borneo (Sarawak).

VII.—FAMILY GASTROMYZONIDAE.

Fishes of the family Gastromyzonidae are small loach-like, hill-stream fishes in which the body is moderately or greatly depressed and the ventral profile is straight and horizontal. Paired fins are horizontally placed and the number of unbranched rays in each is only one. Outer rays of the paired fins are provided with adhesive pads on the ventral surface to help in adhering to rocks in the swift currents. Mouth is subterminal or inferior. Dorsal and anal fins are short. Body is covered with small cycloid scales which are absent on head and on a part or whole of ventral surface. Lateral line is well marked and always extends to base of caudal fin. Gill-openings are either greatly restricted, extending above base of pectorals or of moderate size, extending to opposite base of pectorals dorsally or in some cases to ventral surface for a short distance. Gill-membranes are united with the isthmus and pseudobranchiae are absent.

Internal Characters.—Subtemporal fossae are very shallow and in highly specialized forms, such as *Gastromyzon*, are hardly recognisable. Basipterygium is without a lateral foramen, but is provided with a lateral horn. A ligament connects medial process of modified rib with lateral horn of basipterygium. Some of the other skull characters which are characteristic of the Gastromyzonidae are :

Premaxilla with a long backwardly directed limb ; median limb of premaxilla does not come to lie dorsally to the median rostral bone. Median rostral flattened and cruciform in shape. The preethmoids are lateral to the ethmoid and bear a crescentic suture in the latter. Lateral rostral, flat and articulates with the anterior edge of the preethmoid. Maxilla articulates with the lateral rostral. A backwardly projecting spine from the basioccipital present. Supraethmoid is comparatively small. Parahyoid shows a wing-like process both anteriorly and posteriorly.

Distribution.—Eastern and Southern China, Formosa, Indo-China and Borneo. No member of the family has yet been recorded from Siam, Burma, India, Malaya Peninsula, Sumatra and Java.

Key to the subfamilies of the family Gastromyzonidae.

I. Gill-openings of moderate size, extending to ventral surface of body for a short distance. .. .. .. *Crossostominae.*

II. Gill-openings small and does not extend to ventral surface of body. *Gastromyzoninae.*

SUBFAMILY CROSSOSTOMINAE.

Fang (1935) recognised seven genera in this subfamily and expressed views on their relationships. Hora and Jayaram (1950) referred *Glaniopsis* Boulenger from Borneo to the Crossostominae. Besides

these, no new genus referrable to this subfamily has been described. Below is given a key to the identification of the different genera of the subfamily Crossostominae.

Key to the genera of the subfamily Crossostominae.

I. Definite rostral groove and rostral fold absent—

A. Rostral barbels 2 pairs—

1. Snout broad, rounded, mouth slightly arched; 7 to 8 rays in pelvics; P. 1/8-12. .. .. *Glaniopsis.*

2. Snout narrow, elongated, mouth greatly arched; 11 rays in pelvics; P. 1/16. .. .. .. *Annamia.*

B. Rostral barbels 13 and in several rows, closely applied to rostral fold forming a fringe round the snout. Barbels long. .. .. *Crossostoma.*

II. Definite rostral groove, partly covered by rostral fold, present. Primary rostral barbels partly covered by fold—

A. Mouth opening small, less than $\frac{1}{4}$ in width of head; strongly curved, nearly horse-shoe shaped. Two pairs of rostral barbels (P. 1/16-18; V. 1/8-10).

1. Ventral surface before and between pectorals devoid of scales. Rostral barbels produced from posterior edge of rostral fold; horse-shoe shaped rostral groove not well differentiated. P. 1/16; V. 1/8. .. .. *Liniparhomaloptera.*

2 Ventral surface before pelvics totally scaleless. Rostral barbels well separated from rostral fold. Horse-shoe shaped rostral groove extending posteriorly being divided at latero-posterior to mouth angle. P. 1/16-18; V. 1/10. .. .. *Parhomaloptera.*

B. Mouth opening of moderate size; more than $\frac{1}{4}$ in width of head; crescent shaped. Rostral barbels 4 to 13 in one, two or three rows. (P. 1/12-15; V. 1/8).—

1. 4 rostral barbels in one row; rostral fold distinctly trilobate; ventral side of body scaly, except before and between base of pectoral. .. .. *Vanmanenia.*

2. 7 to 13 rostral barbels in two or three rows. Five distinct or more indistinct lobes in the rostral fold. Ventral side of body upto one-third, anterior part of abdomen scaleless.

a. 7 rostral barbels in two indefinite rows . *Praeformosania.*

b. 13 rostral barbels in two regular or three indefinite rows. .. .. .. *Formosania.*

Glaniopsis Boulenger.

1932. *Glaniopsis*, Hora, *Mem. Ind. Mus.*, **12**, p. 268.

1950. *Glaniopsis*, Hora & Jayaram, *Rec. Ind. Mus.*, **48**, p. 85.

For the diagnostic features of *Glaniopsis* Boulenger, reference may be made to the key for the genera on page 220. Recently Hora and Jayaram (*loc. cit*) redefined this genus from large series of specimens examined by them.

Distribution.—Borneo (Mount Kina Balu).

Glaniopsis hanitschi Boulenger.

1932. *Glaniopsis hanitschi*, Hora, *Mem. Ind. Mus.*, **12**, p. 268.
1950. *Glaniopsis hanitschi*, Hora & Jayaram, *Rec. Ind. Mus*, **48**, p. 85.

D. 2/6-7 ; A. 1/5 ; P. 1/8-12 ; V. 1/7-8 ; C. 16-17.

Head contained 5 to 5·5 and depth of body 7 to 8·5 in total length. Head about as broad as long. Eyes small, diameter contained 5 to 8 in head ; 2 to 4 in snout and 2 to 3 in interorbital space. Least depth of caudal peduncle equals its length.

Locality.—Borneo (Mount Kina Balu).

Specimens examined :—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 676/2	Mt. Kina Balu, Borneo	Mus. Comp. Zool. Mass. Camb. U.S.A.	9 specimens.
F. 677/2	Do.	Do.	61 specimens.
F. 678/2	Do.	Do.	90 specimens.
F. 679/2	Do.	Do.	9 specimens.
F. 683/2	Do.	Do.	80 specimens.
F. 684/2	Do.	Do.	16 specimens.

Annamia Hora.

1930. *Parhomaloptera*, Hora (in part), *Ann. Mag. Nat. Hist.*, (10), **6**, p. 528-586.
1932. *Annamia*, Hora, *Mem. Ind. Mus.*, **12**, p. 306.

For a detailed description of this genus reference may be made to Hora (1932, p. 306).

Genotype.—Annamia normani (Hora).

-Indo-China (Kontum in Annam).

Annamia normani (Hora).

1930. *Parhomaloptera normani*, Hora, *Ann. Mag. Nat. Hist.*, (10), **6**, pp. 582-586, pl. xv. (*Type specimen in British Museum*).
1932. *Annamia normani*, Hora, *Mem. Ind. Mus.*, **12**, p. 307.

D. 2/8 ; A. 1/5 ; P. 1/16 ; V. 1/10 ; C. 18.

Head contained 5·1 and depth of body 10·2 in standard length. Greatest width of head about two-thirds and height about two-fifths in its length. Snout more than half length of head. Diameter of eye contained 4·3 in head ; 2·3 in snout and 1·3 in interorbital width. Least depth of caudal peduncle contained 2 to 2·5 in its length.

Locality.—Indo-China (Kontum in Annam).

Crossostoma Sauvage.

1932. *Crossostoma*, Hora, *Mem. Ind. Mus.*, **12**, p. 307.
1932. *Crossostoma*, Tchang, *Bull. Fan. Mem. Inst. Biol. Peiping*, **3**, pp. 121-125.
1934. *Crossostoma*, Herre, *Lingnan Sci. Journ. Canton*, **13**, p. 285.
1935. *Crossostoma*, Fang, *Sinensia*, **6**, pp. 44-97.
1943. *Crossostoma*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 227.
1949. *Crossostoma*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2** (4), p. 164.

For a detailed description of the genus reference may be made to Hora (*op. cit.*)

Genotype.—*Crossostoma davidi* Sauvage.

Distribution.—China (Fukin ; Kwantung).

Remarks.—Hora (1932) redefined *Crossostoma* and recognised three species under it. Fang (1935) opined that *Crossostoma* was monotypic, being known only from *C. davidi* Sauvage. Herre (1934) described *C. tinkhami* from Kwantung in China. Herre's species is identical with *C. fascicauda* Nichols. *C. stigmata* Nichols (1926) was described from juvenile specimens, but recently Hora (1950) after examining specimens of *C. stigmata* has found it to the conspecific with *C. fascicauda*. Fang (1935) assigned *C. fascicauda*, *C. stigmata* and *C. tinkhami* to the genus *Formosania* Oshima. Chen & Liang (1949) followed Fang's classification. After examining the excellent series of specimens of *C. fascicauda* and a few specimens of *C. davidi* in the collection of the Zoological Survey of India, Indian Museum and comparing them with the type species of *Formosania*, *viz.*, *F. lacustre* (Steind.), I find that the species *fascicauda* belongs to *Crossostoma* and not to *Formosania*. The absence of a rostral groove, the well developed rostral barbels etc., easily distinguish *Crossostoma* from *Formosania*. Thus at present, *Crossostoma* is known from two species, *viz.*, *C. davidi* Sauvage and *C. fascicauda* Nichols, while the genus *Formosania* is monotypic.

Key to the species of the genus Crossostoma *Sauvage.*

I. Rostral barbels well developed ; Maxillary barbels much longer than diameter of eye .. .. *C. davidi.*

II. Rostral barbels short ; Maxillary barbels as long as or shorter than diameter of eye .. .. *C. fascicauda.*

Crossostoma davidi Sauvage.

1932. *Crossostoma davidi*, Hora, *Mem. Ind. Mus.*, **12**, p. 308, pl. xii, fig. 5.
1932. *Crossostoma davidi*, Tchang, *Zool. Sinica*, (B), **2**, fasc 1, pp. 220-221, fig. 115.
1935. *Crossostoma davidi*, Fang, *Sinensia*, **6**, (1), p. 89, fig. 3.
1943. *Crossostoma davidi*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 228.
1949. *Crossostoma davidi*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2** (4), p. 164.
1950. *Crossostoma davidi*, Hora, *Rec. Ind. Mus.*, **48**, p. 48.

D. 3/8 ; A. 3/5 ; P. 1/13-15 ; V. 1/8 ; L. l. 95-108 ; L. tr. $17\frac{1}{2}$-$18\frac{1}{2}$/$13\frac{1}{2}$-$14\frac{1}{2}$.

Head 4·1, depth of body 7·3 and width of body 6·5 in standard length. Width of head 1·33 to 1·5 in its length. Snout in head 1·7 to 2·5 ; interorbital space 2·5 to 3·25 ; depth of caudal peduncle 2·13 to 2·9 and its length 1·57 to 1·9. Diameter of eye in head 8·2 ; in snout 4·5 and 3·1 in interorbital space. Width of mouth 1·06 in snout.

Locality.—China (West Fukien, Yenping, Chung-an-hsien, Foochow and South Chekiang).

Specimens examined :—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens and state of preservotion.*
F. 12231/1	Fukein, China.	P. W. Fang.	1 specimen, Caudal fin damage.
F. 660/2	Do.	Amer. Mus. Nat. Hist.	2 specimens.

Crossostoma Fascicauda Nichols.

1926. *Crossostoma (Formosania) fascicauda*, Nichols, *Amer. Mus. Novit.* No. 224, pp. 2-3, fig. 2.

1926. *Crossostoma (Formosania) stigmata*, Nichols, *Amer. Mus. Novit.*, No. 224, p. 4, fig. 3.

1928. *Crossostoma fascicauda*, Nichols, *Bull. Amer. Mus. Nat. Hist.*, **43**, p. 45.

1928. *Crossostoma stigmata*, Nichols, *Ibid.*, **43**, p. 45.

1932. *Crossostoma fascicauda*, Hora, *Mem. Ind. Mus.*, **12**, p. 308.

1932. *Crossostoma stigmata*, Hora, *Mem. Ind. Mus.*, **12**, p. 308, pl. x, fig. 12.

1933. *Crossostoma fascicauda*, Tchang, *Zool. Sinica* (B), **2**, fasc. 1, pt. 1, p. 220.

1934. *Crossostoma tinkhami*, Herre, *Lingan Sci. Journ.*, **13**, p. 285.

1934. *Formosania fascicauda*, Fang, *Sinensia*, **6**, (1), pp. 83-83, fig. 12-13.

1934. *Formosania stigmata*, Fang, *Sinensia*, **6**, (1), pp. 85-87, fig. 14.

1943. *Crossostoma foscicauda*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 229, fig. 122.

1949. *Formosania fascicauda*, Chen & Liang, *Qvart. Journ. Taiwan Mus.*, **2** (4), p. 164.

1949. *Formosania stigmata*, Chen & Liang, *Ibid.*, **2** (4), p. 164.

1950. *Crossostoma fascicauda*, Hora, *Rec. Ind. Mus.*, **48**, pt. 1, p. 48.

D. 3/8 ; A. 3/5 ; P. 1/14-15 ; V. 1/8 ; L. 1·90-104 ; L. tr. $21\frac{1}{2}/10\frac{1}{2}$-$12\frac{1}{2}$.

Head contained 4·52 ; depth of body 6·28 and width of body 5·73 in standard length. Snout in head 1·81 ; interorbital width 2·71 to 2·8 ; depth of caudal peduncle 2·11 to 2·4 and its length 1·47 to 1·54. Diameter of eye 7 in head. Width of mouth 2·2 in snout.

Locality.—China (Fuching-hsien, Chungan-hsien, Fukien ; Loa-fan-shan, Kwantung).

Specimens examined :—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 661/2	Near Yenping, Fukien, China.	Amer. Mus. Nat. Hist.	4 specimens.
F. 663/2	Chungan Hsien, Fukien, China.	Do.	4 specimens.
F. 662/2	Near Yenping, Fukien, China.	Do.	2 specimens

Liniparhomaloptera Fang.

1935. *Liniparhomaloptera*, Fang, *Sinensia*, **6**, (1), p. 93.

1943. *Liniparhomaloptera*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 223.

1949. *Liniparhomaloptera*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4) p. 164.

I am redefining this Chinese monotypic genus from a number of specimens that I have examined recently :—

Snout broadly pointed and covered with a number of sensory pores. Mouth small, inferior and lunate. Upper lip fleshy, partly overhanging jaw and mouth. Lower lip fleshy, but leaves considerable part of jaw uncovered. Middle part of lip raised into tubercles while its posterior part on each side is produced into short barbel-like processes. Lips continuous at angles of mouth. V-shaped groove at each corner of mouth extending forwards as far as base of last rostral barbel. Rostral fold does not cover upper lip, but is produced into 7 barbels, one median and 3 on either side, the last pair being longest. A pair of well developed maxillary barbels present. Gill-openings extend to ventral surface for short distance. Body covered with small scales which are greatly reduced and faintly marked on ventral surface. Dorsal commences ahead of pelvics and its origin is almost equidistant from tip of snout and base of caudal fin. Pectorals 1/16 and Pelvics 1/8. Pectorals separated from pelvics by considerable distance. Pelvics extend beyond anal opening. Caudal slightly emarginate, lower lobe considerably longer than upper.

Genotype.—*Liniparhomaloptera disparis* (Lin).

Distribution.—China (Lou-fan-shan, Kwantung) and Hong Kong.

Remarks.—First ascribed to *Parhomaloptera* (Lin, 1934), *P. disparis* was redescribed under a new genus, *Liniparhomaloptera* by Fang (1935). *Liniparhomaloptera* is confined to China, whereas, *Parhomaloptera* is found in Borneo. In dealing with the 'Parallel evolution in the cross-ostomoid fishes of the mainland of Asia and the island of Boreno' Hora (1951), enumerates as many as five important differences distinguishing these two genera.

Liniparhomaloptera disparis (Lin,)

1934. *Parhomaloptera disparis*, Lin, *Lingnan Sci. Journ.*, **13**, (2), pp. 225-227, fig. 1-4

1935. *Liniparhomaloptera disparis*, Fang, *Sinensia*, **6**, (1), pp. 94-96.

1949. *Liniparhomaloptera disparis*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 164.

D. 3/7/1 ; A. 3/5/1 ; P. 1/16 ; V. 1/8 ; L. 1.69 ; L. tr. $16\frac{1}{2}/11\frac{1}{2}$.

Head 4·56 and depth of body 5·69 in standard length. Width of head 1·28 ; snout 1·8 and interorbital width 2·25 in length of head. Diameter of eye 6·0 in head. Least depth of caudal peduncle 2 and its length 1·5 in length of head. Dorsal commencing slightly ahead of pelvic origin.

Locality :—China (Lou-fan-shan ; Kwantung ; Hong Kong).

A paratype of this type species in the collection of the Zoological Survey of India, has been lost, most probably in the floods of the Varuna River at Banaras in September 1943. I have examined the following specimens of this species.

Specimens examined.—

Register No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 658/2	White cloud mountain, Canton, China.	Nat. Hist. Mus. Stanford univ.	1 specimen.
F. 659/2	Pok Fulam Reservoir, Hongkong.	Nat. Hist. Mus. Stanford univ.	

Parhomaloptera Vaillant.

1930. *Parhomaloptera*, Hora (in part), *Ann, Mag. Nat. Hist.*, (10) p. 584.

1932. *Parhomaloptera*, Hora , *Mem. Ind. Mus.*, **12**, p. 313.

The genus *Parhomaloptera* is monotypic, being known from the type and only species *P. microstoma*, of Borneo. The diagnostic characters of *Parhomaloptera* are given in the key for the genera on page 220. For a detailed description reference may be made to Hora's monograph (Hora, 1932, *loc. cit.*).

Genotype.—*Parhomaloptera microstoma* (Boulenger).

Distribution.—Borneo (Upper Mahakam river ; Sarawak).

Parhomaloptera microstoma (Boulenger).

1932. *Parhomaloptera microstoma*, Hora, *Mem. Ind. Mus.*, **12**, p. 313, pl. xii fig. 7.

D. 2/7 ; A. 2/5 ; P. 1/16-19 ; V. 1/10 ; L. 1. 100 ; L. tr. 17/1/13.

Head 5·2 in standard and 6·5 in total length. Head much longer than broad. Width 0·75 ; its height 0·5 in its length. Snout more than half length of head. Eyes small, diameter contained 5·6 in head, 3·2 in snout and 2·76 in interorbital width. Dorsal commences in advance of pelvics. Dorsal origin nearer tip of snout than to base of caudal.

Locality.—Borneo (Upper Mahakam River ; River Akar, Sarawak).

Specimens examined.—

Reg. No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 11087/1	Upper Mahakam, Borneo.	Rijks Mus. Nat. Hist. Leyden.	1 specimen.

Vanmanenia Hora.

1932. *Vanmanenia*, Hora, *Mem. Ind. Mus.* **12**, pp. 209-311.

1933. *Homaloptera*, Tchang (in part), *Zool. Sinica*, (B), 2, (1), p. 151.

1935. *Vanmanenia*, Fang, *Sinensia*, 6, (1), p. 57.

1949. *Vanmanenia*, Chen & Liang, *Qurt. Journ. Taiwan Mus.*, 2, (4), p. 163.

For a detailed diagnosis of this genus reference may be made to Hora (1932).

Genotype.—*Vanmanenia stenosoma* (Boulenger).

Distribution.—China (Ningpo river ; Fukein).

Remarks.—Hora (op. cit.), erected the genus *Vanmanenia* to accommodate Boulenger's *Homalosoma stenosoma*—(*Homaloptera stonosoma*). He provisionally assigned *Homaloptera caldwelli* Nichols

(1925), to *Vanmanenia*. *Vanmanenia* resembles the genus *Formosania* Oshima, but the latter seems to be more specialised for life in rapid waters and consequently its rostral groove and fold and paired fins show special modifications.

Key to the species of the genus Vanmanenia *Hora.*

I. Scales less than 101 in lateral line; head vermiculate with black; sides of body without longitudinal stripe .. .. *V. stenosoma.*

II. Scales about 150 in lateral line; head uniformly dark; sides of body with a black stripe from behind head to base of caudal fin. .. .. *V. caldwelli.*

Vanmanenia stenosoma (Boulenger).

1932. *Vanmanenia stenosma*, Hora, *Mem. Ind. Mus.*, **12**, p. 309, pl. xi, fig. 9.

1932. *Homaloptera (Homalosoma) caldwelli chekianensis*, Tchang, *Bull. Fan. Mem. Inst. Biol.*, **3**, (6), p. 83-84.

1933. *Homaloptera caldwelli chekianensis*, Tchang, *Zool. Sinica*, (B), **2**, fasc I. (1), p. 219, fig. 114.

1935. *Vanmanenia stenosoma*, Fang, *Sinensia*, **6**, pp. 58-68, fig. 7.

1939. *Vanmanenia stenosoma*, Wu, *Sinensia*, **10**, p. 127.

1949. *Vanmanenia stenosoma*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 163.

D. 3/7 ; A. 3/5-6 ; P. 1/13-14 ; V. 1/7 ; L. 1.94-101 ; L. tr. 21½/15½.

Head about 5 and depth of body 5·8 to 6·7 in total length. Width of head 1·29 in its length. Snout 1·83 to 1·9 and interorbital space 2·17 to 2·44 in head. Diameter of eye 6·47 to 6·5 in head. Depth of caudal peduncle about equal to its length. Width of mouth 2·2 in length of snout.

Locality.—China (Ningpo; kikow; Feughua, Hsia-Chiaokow near West Tien-mu-Shan; Lau-chie, Chen-hsien, and Tien-tai in Chekian Province).

Vanmanenia caldwelli (Nichols).

1925. *Homaloptera caldwelli*, Nichols, *Amer, Mus. Novit.*, No. 172, p.1.

1935. *Vanmanenia caldwelli*, Fang, *Sinensia*, **6**, (1), p. 68, fig. 8.

1949. *Vanmanenia caldwelli*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 163.

D. 3/8 ; A. 3/5 ; P. 1/13-14 ; V. 1/6-7 ; L. 1.150.

Head contained 4·75 to 5 and depth of body 6·75 to 7 in standard length. Snout more than half length of head. Diameter of eye contained 4·25 to 5·25 in head; 2·25 to 3 in snout and 2·4 in interorbital width Prenasal part of snout about equal to interorbital width. Commencement of dorsal ahead of pelvics, and its origin is nearer to tip of snout than to base of caudal fin. Anal reaches base of caudal. Sides of body with a black stripe from shoulder to base of caudal.

Locality.—China (Yenping, Chungan, Fukein).

I have examined the following specimens in the collection of the Zoological Survey of India, Indian Museum :—

Reg. No.	*Locality.*	*Donor or Collector.*	*No. of Specimens.*
F. 664/2	Yenping, Fukein, China.	Amer. Mus. Nat. Hist.	1 specimen.
F. 665/2	Chungan, Hsien, Fukein, China.	Do.	3 specimens.

Praeformosania FANG.

1935. *Praeformosania*, Fang, *Sinensia*, **6**, (1), p. 71.

1943. *Praeformosania*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 226.

1949. *Praeformosania*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 164.

To facilitate reference in future a short description of this genus is given below :—

Snout broad, rounded and much longer than postorbital part of head Mouth small, inferior and crescent shaped. Lips fleshy, but at angles of mouth are thin and continuous. Rostral groove continuous at angles of mouth. Seven rostral barbels, four primary and three secondary and minute, slightly anteriorly placed thus forming two distinguishable series. Six minute triangular lobes present before secondary rostral barbels. Scales small, covering body except on head and ventral surface of body between and in front of pectorals. Gill-openings extend to ventral surface for a short distance. Dorsal commences slightly in advance to pelvics. Pectorals begin behind eye and are separated from pelvics by a considerable distance. Pelvics reach anal opening but fall much short of anal fin. Pectorals with 15 to 16 rays and pelvics with 9 rays of which the outer one ray is simple. Pelvic provided with a fleshy appendage in its axil. Caudal somewhat emarginate, lower lobe being slightly longer than upper.

Genotype.—Praeformosania pinchowensis Fang.

Distribution.—China (Ping-chow-hsien, Hu-yuan-hsien, South Kweichow ; Kwang-lau, Lin-yuen-hsien, North Western Kwangsi).

Remarks.—Fang (1935) described three species of *Praeformosania, viz., P. pinchowensis, P. intermedia* and *P. lineata.* Later Wu, (1939) in describing *Formosania yaoshanensis* from Yao-shan observed : "The new species appears to be in close relation with the species of *Praeformosania,* as noted by Fang and *Formosania stigmata,* but differs from the latter in the colouration." *F. stigmata* as shown above (*vide supra,* p.222) is con-specific with *Crossostoma fascicauda* (Nichols). Moreover, *Crossostoma* is easily distinguished from *Formosania* in the absence of a definite rostral groove. The description of *F. yaoshanensis* leaves little in doubt about its Praeformosanian characters, and in view of its considerable similarity to *P. lineata,* it is treated here as a synonym of the latter.

Key to the species of the genus Praeformosania *Fang.*

I. Distance from vent to anal ½ that from vent to pelvic axil. (Body marbled with blackish or more or less marked with pale centred rings of same colour on dorsal surface and sides. L. 1. 102.) .. *P. pingchowensis.*

Distance from vent to anal two-third or four-fifth that from vent to pelvic axil.

A. Body and cadual peduncle marked with alternatively arranged dark blotches; L. l. 97 to 102 .. .. *P. intermedia.*

B. Body and caudal peduncle with two dark brownish dorso-lateral stripes, extending from head to base of caudal on each side. L. l. 88 to 92. .. .. .. *P. lineata.*

Praeformosania pingchowensis Fang.

1935. *Praeformosania pingchowensis*, Fang, *Sinensia*, **6**, (1), p. 72, fig. 3c and 9.

1943. *Praeformosania pingchowensis*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 226.

1949. *Praeformosania pingchowensis*, Chen & Liang, *Quart. Journ. Taiwan Mus.*) **2**, (4), p.164.

D. 3/8; A. 3/5; P. 1/5; V. 1/8; L. 1.102; L. tr. 22/11.

Head contained 4·6 to 4·8 and depth of body 6·7 to 6·9 in standard length. Diameter of eye in head 6·3 to 6·6. Width of head in its length 1.19; snout 1·73 and interorbital 2·64. Depth of caudal peduncle in head 2·73 and its length 1·9 to 2·7. Width of mouth in snout 2·3. For a detailed description of this type species reference may be made to the description of the genus.

Locality.—China (Pingchow-hsien, Southern Kweichow; Mountain streams of Si-kiang or West River).

Praeformosania intermedia Fang.

1935. *Praeformosania intermedia*, Fang, *Sinensia*, **6**, p. 75, fig. 10.

1943. *Praeformosania intermedia*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 226.

1949. *Praeformosania intermedia*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 164.

D. 3/9; A. 3/5/1; P. 1/14; V. 1/8; L. 1.97—102; L. tr. 20½/12½.

Head contained 4·82 and depth of body 5·5 to 6·62 in standard length. Width of head 1·28; snout 1·83 and interorbital width 2·75 in its length. Diameter of eye 4·4 in head. Depth of caudal peduncle 2·2 in head and its length 1·57. Width of mouth in snout 2·0.

Locality.—China (Tu-yuen-hsien, Southern Kweichow; Mountain streams running into Tungting Lake).

Praeformosania lineata Fang.

1935. *Praeformosania lineata*, Fang, *Sinensia*, **6**, (1), p. 78, fig. 11.

1939. *Formosania yaoshanensis*, Wu, *Sinensia*, **10**, (1-6), p. 128, pl. iii, fig. 7.

1943. *Praeformosania lineata*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 226.

1949. *Praeformosania lineata*, Chen & Liang, *Quart. Journ. Taiwan. Mus.*, **2**, (4), p. 164.

D. 3/8; A. 3/5; P. 1/15; V. 1/8; L. 1. 8-92; L. tr. 19½/12½.

Head contained 4·86 and depth of body 5·67 in standard length. Width of head 1·17; snout 1·57 and interorbital space 2 in its length. Diameter of eye 7 in head. Depth of caudal peduncle 1·75 in head and its length 1·27. Width of mouth in snout 2.

Locality.—China (Kwang-Lau, Ling-yuew-hsien, North Western Kwangsi ; Yao-shan, Likiang).

Formosania OSHIMA.

1932. *Formosania*, Hora, *Mem. Ind. Mus.*, **12**, p. 311.
1935. *Formosania*, Fang, *Sinensia*, **6**, (1), p. 80.
1943. *Crossostoma*, Nichols (in part), *Nat. Hist. Central Asia*, **9**, p. 228.
1949. *Formosania*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (1), p. 164.

For a complete diagnosis of this genus reference may be made to Hora (1932) and Fang (1935). The sailent characters of the genus are given in the key for the genera on page 220.

Genotype.—*Formosania lacustre* (Steindachner).

Distribution.—Formosa (Tamusi river near Lake Candidius).

Remarks.—The monotypic nature of *Formosania* has been referred to already (*vide supra p.* 222). The genus shows affinities to *Vanmanenia* and *Praeformosania*, but is more specialised than them. The presence of a rostral groove and the shorter barbels and their disposition easily distinguishes *Formosania* from *Crossostoma*, with which genus it was confused by some of the earlier workers.

Formosania lacustre (Steindachner.)

1932. *Formosania lacustre*, Hora, *Mem. Ind. Mus.*, **12**, p. 311, pl. xii, fig. 6.
1934. *Formosania lacustre*, Fang, *Sinensia*, **6**, (1) pp. 82-83.
1949. *Formosania lacustre*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 164.

D. 3/8 ; A. 3/5 ; P. 1/14-15 ; V. 1/8 ; L. 1. 113 ; L. tr. $25\frac{1}{2}/15\frac{1}{2}$.

Head contained 4·7 and depth of body 6·3 in standard length. Width of head 1·2 ; snout 1·79 and eye 8·0 in head. Interorbital space 2·5 in length of head. Depth of caudal peduncle 1·75 in head and its length 1·5. Width of mouth 2·25 in snout.

Specimens examined :—

Reg. No.	*Locality.*	*Donor or Collector.*	*No. of Specimens.*
F. 1189/1	Lake Candidius, Formosa.	British Museum.	1 Specimen.

SUBFAMILY GASTROMYZONINAE.

Fishes of the subfamily Gastromyzoninae are confined to Indo-China, China, Formosa and Borneo. On geographical grounds as well as on taxonomical considerations, the subfamily is divided into two divisions. Thus the four genera confined to the mainland of Asia are grouped under *Pseudogastromyzoni* and those found in Borneo under *Gastromyzoni*.

Key to the divisions of the subfamily Gastromyzoninae.

I. Pectorals extending beyond commencement of pelvics. Width of mouth less than $\frac{1}{3}$ in width of head. (Mainland of Asia) .. .. .. *Pseudogastromyzoni*.

II. Pectorals separated from pelvics by a considerable distance. Width of mouth more than $\frac{1}{3}$ width of head. (Borneo) .. .. *Gastromyzoni*.

Division I. *Pseudogastromyzoni*.

Below is given a key to the identification of the different genera of the division Pseudogastromyzoni :

I. Four rostral barbels, plate-like at their bases, provided with fringed edges and terminating in short barbel-like processes ; bases of the two anterior barbels united .. .. *Sewellia*.

II. Four rostral barbels, plain and distinct from each other.

A. Pelvics free from each other and not united to form a disc-like structure.

1. Gill-opening extends to opposite base of pectoral fin .. .. *Paraprotomyzon.*

2. Gill-opening situated entirely above base of pectoral fin .. .. *Pseudogastromyzon.*

B. Pelvics united posteriorly to form a disc-like structure .. .. *Beaufortia.*

Sewellia Hora.

1932. *Sewellia,* Hora, *Mem. Ind. Mus.*, **12**, pp. 315-317.

For a detailed description of this remarkable genus reference may be made to Hora's monograph (Hora, 1932, p. 315).

Genotype.—Sewellia lineolata (Val.).

Distribution.—Indo-China.

Remarks.—Since the publication of his Memoir on the Homalopterid fishes (Hora, 1932), no further material has been described under the genus *Sewellia.* Hora (1932), Fang (1933), and Hora (1951) have expressed opinions of the phylogenetic relationships of this remarkable genus. *Sewellia* is a highly specialised form and differs considerably from the Chinese Pseudogastromyzoni. The genus is monotypic.

Sewellia lineolata Valenciennes.

1846. *Balitora lineolata,* Valenciennes, *Hist. Nat. Poiss.*, **18**, p. 99.

1932. *Sewellia lineolata,* Hora, *Mem. Ind. Mus.*, **12**, p. 317. pl. xi, fig. **10**, pl. xii, fig. 10.

D. 9 ; A. 5 ; P. 1/21 ; V. 1/17 ; C. 23 ; L. 1. 46-50.

Head contained 5·6 to 5·9 in total and 4·4 to 4·6 in standard length. Eyes moderately large, diameter contained 3·5 in head, 2 in snout and 1·75 in interorbital width. For a detailed description of this type and only species reference may be made to Hora (*loc. cit.*).

Specimens examined :—

Reg. No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 11291/1	Cochin, China.	Mus. National Hist. Nat. Paris.	1 specimen.

Paraprotomyzon Pellegrin & Fang

1935. *Paraprotomyzon,* Pellegrin & Fang, *Sinensia,* **6**, pp. 99-107.

1936. *Paraprotomyzon,* Pellegrin & Fang, *Absta. Pap. Sci. Conf. Nanking,* p. 665.

1949. *Paraprotomyzon,* Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 165.

1950. *Paraprotomyzon,* Hora & Jayaram, *Rec. Ind. Mus.*, **48** (2), p. 61.

The genus *Paraprotomyzon* is redefined here as follows :—

Snout broad, rounded and spatulate ; covered with rudimentary warts and sensory pores. Mouth inferior, and cresent shaped. Upper jaw covered by a lip, but anterior sharp rasping edge of lower jaw

exposed. Lips continuous at angles of mouth. Rostral fold prominent and distinctly trilobate. Six barbels, four rostral and two maxillary. Rostral barbels situated in between lobes of rostral fold. Gill-opening extends to opposite base of pectoral fin. Scales small, cycloid, absent from ventral surface of body before base of pelvic fin. Lateral line complete. Paired fins horizontal, fairly extensive and provided with oblique muscular bases. Pectorals commence behind eye and extend beyond origin of pelvic fin. Pelvics commence slightly in advance to dorsal and extends beyond anal opening. Pectoral with 19 and pelvic with 14 branched rays. Pelvics free from each other, not uniting to form a disc-like structure. Caudal obliquely truncate, with the lower lobe slightly longer.

Genotype.—*Paraprotomyzon multifasciatus* Pellegrin & Fang.

Distribution.—China (Kwai-Chow, Eastern Szechuan).

Paraprotomyzon multifasciatus Pellegrin & Fang.

1935. *Paraprotomyzon multifasciatus*, Pellegrin & Fang, *Sinensia*, **6**, pp. 103-107, fig. 1-2.

1936. *Paraprotomyzon multifasciatus*, Pellegrin & Fang, *Absts. Pap. Sci. Conf, Nanking*, P. 665.

1949. *Paraprotomyzon multifasciatus*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 165.

1950. *Paraprotomyzon multifasciatus*, Hora & Jayaram, *Rec. Ind. Mus.*, **48** p. 16.

D. 3/7 ; A. 3/5 ; P. 1/19 ; V. 1/14 ; L. 1. 69-74 ; L. tr. $22\frac{1}{2}$/14-$16\frac{1}{2}$.

Head 4·29 to 5 and depth of body 5·3 to 5·72 in standard length. Width of head in its length 0·93. Diameter of eye in head 6 to 7 and 4 in snout. Snout 1·62 to 1·71 and interorbital space 1·62 to 1·78 in head. Least depth of caudal peduncle 1·9 to 2·5 in head and its length 1 to 1·27. Width of mouth 1·8 to 2·3 in snout.

Locality.—China (Kwai-chow, Eastern Szechuan).

Specimens examined :—

Reg. No.	*Locality.*	*Donor or Collector.*	*No. of specimens.*
F. 669/2	Kouri-Tcheon China.	Mus. National Hist. D' Paris.	1 specimen.

Pseudogastromyzon Nichols.

1932. *Pseudogastromyzon*, Hora, *Mem. Ind. Mus.*, **12**, pp. 313-315.

1933. *Pseudogastromyzon*, Fang, *Sinensia*, **4**, **(3)**, p. 39.

1938. *Pseudogastromyzon*, Herre, *Lingnan Sci. Journ.*, **17** (3), p. 428.

1943. *Pseudogastromyzon*, Nichols, *Nat. Hist. Central Asia*, **9** p. 230.

1949. *Pseudogastromyzon*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 165.

For a complete diagnosis of this remarkable genus reference may be made to Hora (1932) and Fang (1933). The salient features of the genus are given in the key on page. 220.

Genotype.—*Pseudogastromyzon fasciatus* (Sauvage).

Distribution.—China (Chung-hsein, N. Fukien ; Canton ; S. Chekiang ; Changting-hsien, Fukien ; Hong Kong ; Tungpei Shin, Lieuhsien, Kwan-tung).

Remarks.—Four species and a subspecies have been added to this genus since 1932. Fang (1933) referred *Crossostoma fangi* of Nichols (1931) to *Pseudogastromyzon.* He also gave a redescription of the type species *P. fasciatus* (Sauvage). Herre (1932) described *P. myersi* from Hong Kong. Liang (1942) reported the discovery of a new species and a subspecies of *Pseudogastromyzon, viz., P. cheni,* and *P. fasciatus changtingensis* from Fukien, China. Chen & Liang (1949) described *P. tungpeiensis* from Kwantung, China.

Key to the species of the genus Pseudogastromyzon *Nichols.*

I. Each lobe of trilobed rostral fold provided with 5 papillae along its free border.

- A. Scales on lateral line 85; V. 1/10; P. 1/18-19; horizontal portion of pectorals with uniserial warty points arranged from base to the tip .. .. .. *P. fasciatus.*
- B. Scales on lateral line 76-78; V. 1/8; P. 1/19-20; pectorals without warty points on the rays .. .. *P. fasciatus changtingensis.*

II. Each lobe of trilobed rostral fold not provided with 5 papillae along its free border.

- A. Pectorals with 16 branched rays.
  1. Later line 70; V. 1/8 .. .. *P. myersi.*
  2. Lateral line 73-77; V. 1/9 (each lobe of rostral fold provided with 3 papillae along its free border). *P. cheni.*
- B. Pectorals with 18 or more branched rays.
  1. Lateral line 73; P. 1/18; each lobe of rostral fold provided with 4 papillae along its free border .. *P. tungpeiensis.*
  2. Lateral line 96; P. 1/19; each lobe of rostral fold divided into two flat and somewhat barbel shaped lobules a long its free border .. *P. fangi.*

Pseudogastromyzon fasciatus (Sauvage).

1932. *Pseudogastromyzon fasciatus*, Hora, *Mem. Ind. Mus.*, **12**, p. 314, pl. xii, fig. 8-9.

1933. *Pseudogastromyzon fasciatus*, Fang, *Sinensia*, **4**, (3), pp .41.

1943. *Hemimyzon* (*Pseudogastromyzon*) *zebroides*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 230.

1949. *Pseudogastromyzon fasciatus*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 165.

D. 2/8; A. 1/6; P. 1/18-19; V. 1/10; L. l. 85; L. tr. $18\frac{1}{2}/9—10\frac{1}{2}$.

Head 4·29 and depth of body 6·25 in standard length. Width of head in its length 1·25. Eyes small, diameter contained 6·29 in head. Snout 1·7 and interorbital width 2·12 in head. Caudal peduncle about as long as deep and its length contained 2·12 in head. Width of mouth 1·43 in snout.

Locality.—China (Chungan-hsien, N. Fukien; Canton; and South Chekiang).

Pseudogastromyzon fasciatus changtingensis Liang

1942. *Pseudogastromyzon fasciatus changtingensis*, Liang, *Contr. Res. Ins. Zool, Bot. Fukien Prov. Acad.*, No. 2, pp. 1-8, fig. 2.

1949. *Pseudogastromyzon fasciatus changtingensis*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, 2, (4), pp. 165-166.

D. 2/8 ; A. 2/5-6 ; P. 1/19-20 ; V. 1/8 ; L. 1. 76-78 ; L. tr. $20\frac{1}{2}$-$21\frac{1}{2}$/$7\frac{1}{2}$-$9\frac{1}{2}$.

Head 5·16 to 5·35 and depth of body 4·67 to 5·38 in standard length. Width of head equal to its length. Diameter of eye 5·28 to 6 in head. Snout 1·54 to 1·6 and interorbital width 1·7 to 1·85 in head. Least depth of caudal peduncle 2·11 to 2·16 in head and its length 1·57 and 1·81. Width of mouth 2·5 to 3 in snout.

Locality.—China (Changting-hsien, Fukien).

Remarks.—This subspecies is distinguished from the *forma typica* in the pelvics possessing only 8 branched rays instead of 10 ; absence of warty processes on the base of pectoral rays ; lesser number of pores along the lateral line and fewer vertical bands along the sides of the body.

Pseudogastromyzon myersi Herre.

1932. *Pseudogastromyzon myersi*, Herre, *Lingnan Sci. Journ.*, 2, (3), pp. 430-431.

1938. *Pseudogastromyzon myersi*, Herre, *Ibid.*, 17, (3), p. 428.

1943. *Hemimyzon myersi*, Nichols, *Nat. Hist. Central Asia*, 9, *p.* 230.

1949. *Pseudogastromyzon myersi*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, 2, p. 165.

D. 2/7 ; A. 1/5 ; P. 1/16 ; V. 1/8 ; L. 1. 70.

Head 4·5 and depth of body 8·1 in standard length. Snout 1·6 and interorbital width 2·15 in head. Diameter of eye 4·3 in head. Least depth of caudal peduncle 2·6 in head. Dorsal origin midway between tip of snout and base of caudal. Pectorals overlap pelvics. Pelvics fall considerably short of anal which in turn does not reach caudal fin.

Locality.—Hong Kong and Lantan Islands.

Pseudogastromyzon tungpeiensis Chen & Liang.

1949. *Pseudogastromyzon tungpeiensis*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, 2, (4), p. 158-161, fig. 1.

D. 2/8 ; A. 2/6 ; P. 1/18 ; V. 1/8 ; L. 1. 73 ; L. tr. $21\frac{1}{2}$/$11\frac{1}{2}$.

Head 4·89 and depth of body 6·35 in standard length. Width of head in its length 1·13. Diameter of eye 6·45 in head. Snout 1·59 and interorbital width 2·08 in head. Least depth of caudal peduncle contained 2·0 in head and its length 2·25. Width of mouth in snout 1·89.

Locality.—China (Tungpie-shein, Lienhsien, Kwantung).

Remarks.—From *P. fasciatus* the above species is distinguished by the nature of the rostral fold, the chin adhesive apparatus, the less branched rays of the pelvics and the lesser number of pores along the lateral line. It differs from *P. fangi* in having blackish markings on the dorsal surface of the head and the base of the pectorals. In having larger number of rays in the pectorals (18 *versus* 16) it is distinguished from *P. myersi.*

Pseudogatromyzon cheni Liang.

1942. *Pseudogastromyzon cheni*, Liang, *Contr. Res. Ins. Zool. Bot. Fukien Prov. Acad.*, No. 1, pp. 1-8, fig. 2.

1949. *Pseudogastromyzon cheni*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 166.

D. 2/7 ; A. 2/5 ; P. 1/16 ; V. 1/9 ; L. 1. 73-77 ; L. tr. 16½-20½/9½-11½.

Head 4·64 to 4·89 and depth of body 5·2 to 5·92 in standard length. Width of head in its length 0·9. Diameter of eye 4·3 to 6·74 in head. Snout 1·56 to 1·73 and interorbital space 1·91 to 2·1 in head. Least depth of caudal peduncle 2·21 to 2·6 in head and its length 1·43 to 2·43. Width of mouth 2·6 to 3·4 in head.

Locality.—China (Changting-hsien, Fukien).

Pseudogatromyzon fangi (Nichols).

1931. *Crossostoma fangi*, Nichols, *Lingnan Sci. Journ.*, **10**, p. 263, fig. 1.

1933. *Pseudogastromyzon fangi*, Fang, *Sinensia*, **4**, (3), pp. 46-48, fig. 2.

1943. *Crossostoma fangi*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 299, fig. 123.

1949. *Pseudogastromyzon fangi*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 167.

D. 2/9 ; A. 2/5 ; P. 1/19 ; V. 1/7 ; L. 1. 96 ; L. tr. 23½/10½.

Head 5 and depth of body 6·8 in standard length. Width of head in its length 1·12. Diameter of eye 5·56 in head. Snout 1·6 and interorbital width 1·99 in head. Least depth of caudal peduncle 2·36 in head and its length 1·4. Width of mouth 2·5 in snout.

Locality.—China (Vicinity of Canton, Kwangtung).

Beaufortia Hora.

1932. *Beaufortia*, Hora, *Mem. Ind. Mus.*, **12**, p. 318.

1943. *Gastromyzon*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 231.

1944. *Beaufortia*, Chang, *Sinensia*, **15**, p. 55.

1949. *Gastromyzon*, Chen & Liang, *Quart, Journ. Taiwan Mus.*, **2**, (2), p. 167.

The diagnositic characters of this genus are given in the key on page 230. For a complete description reference may be made to Hora, 1932, (*loc. cit.*).

Genotype.—*Beaufortia leveretti* (Nichols & Pope).

Distribution.—China (Omei, Loochow, Szechuan ; Loshan, and Yann ; San-ho-hsien, Kweichow ; Noda, Hainan ; Lin-yueng-hsien, N.W. Kwangsi ; Tung-Kwei, Lung-Chow, S.W. Kwangsi).

Remarks.—*Beaufortia* is at present known from six species. Since 1932 only one species, *viz.*, *B. liui* Chang (1944) has been added to the

Key to the species of the genus Beaufortia *Hora.*

I. Pelvics extend upto or beyond anal opening.

A. P. 1/22 ; V. 1/16.

1. Scales on lateral line 98 to 102 *B. liui.*

2. Scales on lateral line 112. .. .. *B. zebroidus.*

B. P. 1/24-27 ; V. 1/19-21.

1. Scales on lateral line 75 ; pelvics extend beyond anal opening ; P. 1/25-27 ; V. 1/20-21 .. .. *B. leveretti.*

2. Scales on lateral line 70-72 ; pelvics extend upto anal opening ; P. 1/24-26 ; V. 1/19-20 .. .. *B. kweichowensis.*

II. Pelvics separated considerably from anal opening.

A. Caudal fin obliquely truncate ; P. 1/22-23 ; V. 1/17 .. .. *B. pingi.*

B. Caudal fin distinctly emarginate ; P. 1/25-26 ; V. 1/17-19 *B. szechuanensis.*

Beaufortia liui chang.

1944. *Beaufortia liui*, Chang, *Sinensia*, **15**, p. 55, fig. 3.

D. 3/7 ; A. 2/5 ; P. 1/22 ; V. 1/16 ; L. 1. 98-102.

Head 4·9 and depth of body 4·5 in standard length. Depth of head in its length 1·6 and width 0·9 to 1·0. Diameter of eye 5·3 to 6·6 and interorbital space 2·1 in head. Caudal peduncle 2·1 to 2·2 and its length 2·1 in head.

Locality.—China (Loshan and Yaan, Szechuan).

Beaufortia zebroidus (Fang).

1930. *Gastromyzon pingi zebroidus*, Fang, *Sinensia*, **1**, (3), p. 35, pl. ii, fig. 1-2.

1932. *Beaufortia zebroidus*, Hora, *Mem. Ind. Mus.*, **12**, p. 319.

1943. *Gastromyzon zebroidus*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 231.

1949. *Gastromyzon zebroidus*, Chen & Liang, *Quart. Journ. Taiwan, Mus.*, **2**, (4), p. 167.

D. 2/6 ; A. 2/4-5 ; P. 1/22 ; V. 1/16 ; L. 1. 112.

Head contained 4 times and depth of body 5·4 in standard length. Diameter of eye contained 5·9 to 6 in head.

Locality.—China (Tung-Kwei, Lung-Chown, S.W. Kwangsi).

Beaufortia kweichowensis (Fang).

1931. *Gastromyzon leveretti kweichowensis*, Fang, *Sinensia*, **2**, (3), pp. 41-44, fig. 1.

1943. *Gastromyzon kweichowensis*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 231.

1949. *Gastromyzon kweichowensis*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 167.

D. 2/8 ; A. 2/4 ; P. 1/24-26 ; V. 1/19-20 ; L. 1. 70-72.

Head 4·1 and depth of body 5·4 in standard length. Width of head in its length 1·1. Diameter of eye 6·8 in head. Interorbital width 2·2 and snout 1·48 in head. Depth of caudal peduncle 2·56 in head and its length 2·4. Width of mouth 3·24 in snout.

Locality.—China (San-ho-hsien, Kweichow).

Beaufortia leveretti Nichols and Pope.

1932. *Beaufortia leveretti*, Hora, *Mem. Ind. Mus.*, **12**, p. 319, pl. xii, fig. 11.

1943. *Gastromyzon leveretti*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 231, fig. 125.

1949. *Gastromyzon leveretti*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 167.

D. 2/8 ; A. 2/7 ; P. 1/25-27 ; V. 1/20-21 ; L. 1.75.

Head 4·3 and depth of body 5·3 in standard length. Width of head in its length 1·1. Diameter of eye contained 5·5 in head. Snout 1·8 and interorbital width 2·3 in head. Depth of caudal peduncle 2·25 in head, and its length 2·9. Width of mouth 2·4 in snout.

Locality.—China (Nodoa, Hainan).

Specimens examined.—

Reg. No.	*Locality.*	*Donor or collector.*	*No. of specimens.*
F. 11090/1	Hainan, China . .	Amer. Mus. Nat. Hist.	1 specimen.
F. 670/2	Nodoa, Hainan, China	Do. . .	2 specimens.

Beaufortia pingi (Fang).

1930. *Gastromyzon pingi*, Fang, *Sinensia*, **1**, (3), pp. 31-34, pl. **1**, fig. 3-5.
1932. *Beaufortia pingi*, Hora, *Mem. Ind. Mus.*, **12**, **p.** 319.
1943. *Gastromyzon pingi*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 331.
1949. *Gastromyzon pingi*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 167.

A. 2/4 ; P. 1/22-23 ; V. 1/17 ; L. 1.119.

Head 4·5 and depth of body 5·5 in standard length. Width of head in its length 1·2. Diameter of eye in head 6·25 to 6·5. Snout 2·7 and interorbital width 1·5 to 1·6 in head. Least depth of caudal peduncle about its length. Width of mouth 1·67 in snout.

Locality.—China (Lin-yueng-shien, Kwangsi).

I have examined a topotype of this species in the collection of the Zoological Survey of India as under :—

Reg. No.	*Locality.*	*Donor or collector.*	*No. of specimens.*
F. 11112/1	Kwangsi, China .	P. W. Fang . .	1 specimen.

Beaufortia szechuanensis (Fang).

1930. *Gastromyzon szechuanensis*, Fang, *Contri. Biol. Sci. Soc. China*, *(Zool. Ser.)*, **6**, p. 36, fig. 6-7.
1932. *Beaufortia szechuanensis*, Hora, *Mem. Ind. Mus.*, **12**, p. 319.
1943. *Gastromyzon szechuanensis*, Nichols, *Nat. Hist. Central Asia*, **9**, p. 232.
1949. *Gastromyzon szechuanensis*, Chen & Liang, *Quart. Journ. Taiwan Mus.*, **2**, (4), p. 167.

D. 2/8 ; A. 1/5 ; P. 1/25-26 ; V. 1/17 ; L. 1.137.

Two specimens 78 and 83 mm. in standard length in the collection of the Zoological Survey of India, received recently in exchange from the U. S. National Museum, and labelled *Beaufortia pingi*, on examination have prooved to be *B. szechuanensis*. A short description of this rare species from Szechuan, China, is given below :—

Head contained 5 in standard and 5·7 to 5·9 in total length. Depth of body contained 9·5 in standard and 10·5 to 11 in total length. Snout much more than half length of head. Eyes small diameter, contained

7 in head, 4·75 in snout and 3·3 in interorbital space. Upper lip free from upper jaw. Lower lip notched at its anterior median line where two rounded papillae are present. Four minute rostral barbels present. Maxillary barbels much longer. Dorsal commences behind origin of pelvics. Pectorals begin slightly in front of eyes, and overlap pelvics for a considerable distance. Pelvics united to form a disc-like structure. Pectorals with 26 to 27 rays and pelvics with 18 to 20 rays of which one outer ray in each fin is simple. Vent situated midway between posterior extremity of pelvics and anal fin. A flap of skin adnate to axil of pelvic fin present. Gill-openings restricted to above base of pectoral fin. Colour in alcohol pale brownish on sides and lighter below. Three dark blotches on dorsal surface in front of dorsal fin and 3 to 4 behind it. Caudal with a light brownish marking across.

Locality.—China (Omei, Loochow, Szechuan).

Specimens examined.—

Reg. No.	*Locality.*	*Donor or collector.*	*No. of specimens*
F 671/2	Yachow, Szechuan, China.	U. S. Nat. Mus.	2 specimens.

Division II. GASTROMYZONI.

Pectorals separated from pelvics by some distance. Mouth more than 1/3rd width of head. Below is given a key to the identification of the different genera of the Division Gastromyzoni.

I. Pelvics free from each other, not uniting to form a disc-like structure. Gill-openings restricted to sides, extending to base of pectoral fin dorsally.

A. Gape of mouth considerably less than half width of head; rostral groove and rostral fold absent; rostral barbels fully exposed on ventral surface. *Protomyzon.*

B. Gape of mouth more than half width of head; rostral fold present; rostral fold notched to accommodate four short barbels. .. .. *Progastromyzon.*

II. Pelvics united posteriorly to form a disc-like structure. Gill-openings situated entirely above base of pectoral fin.

A. Breadth of body containd five times in total length without caudal; mouth overhung by a fold bearing rostral barbels. .. .. *Neogastromyzon.*

B. Breadth of body contained 3·2 times in total length without caudal; mouth fully exposed; rostral barbels considerably in front of mouth. .. .. *Gastromyzon.*

Protomyzon Hora.

1932. *Protomyzon*, Hora, *Mem. Ind. Mus.*, **12**, p. 306.

1950. *Protomyzon*, Hora & Jayaram, *Rec. Ind. Mus.*, **47** (2), p. 61.

The diagnostic characters of this genus are given in the above key to the genera of the division *Gastromyzoni.* For a complete description Hora (1932, p. 306) may be consulted.

Genotype.—*Protomyzon whiteheadi* (Vaillant).

Distribution.—Borneo (Mout Kina Balu).

Remarks.—Hora (1932) proposed the genus *Protomyzon* to accommodate *Homaloptera whiteheadi* Vaillant (1893) from Borneo. Recently Hora and Jayaram (1950, *op. cit.*), described a species of *Protomyzon, viz., P. borneensis* from Mount Kina Balu in Borneo. Hora (1951), has expressed views regarding the relationships of this genus to the other genera of the Gastromyzoni.

Key to the species of the genus Protomyzon *Hora.*

I.	Snout broad, rounded ; V. 1/9-10 ; scales absent on ventral surface only between and before base of pectorals ; Lateral line complete.	*P. whiteheadi.*
II.	Snout conical and more or less pointed. V. 1/8 ; scales absent on ventral surface before anal opening. Lateral line incomplete, extending only up to anal fin.	*P. borneensis.*

Protomyzon whiteheadi (Vaillant).

1932. *Protomyzon whiteheadi*, Hora, *Mem. Ind. Mus.*, **12**, p. 306.

1950. *Protomyzon whiteheadi*, Hora & Jayaram, *Rec. Ind. Mus.*, **48**, pt. 2.

D. 1/7 ; A. 1/6-7 ; P. 1/21-22 ; V. 1/9-10 ; C. 15-16.

Head contained 5·5 to 6 and depth of body 8 in total length. Height of head slightly less than length of snout. Eyes small, dorsolateral, diameter contained 6 to 7 times in head ; 2·5 to 3 in snout and 2 to 2·5 in inter-orbital width. Least height of caudal peduncle contained 1·5 in its length.

Locality.—Borneo (Mount Kina Balu).

I have examined the following specimens in the collection of the Zoological Survey of India, Indian Museum :

Reg. No.	*Locality.*	*Donor or collector.*	*No. of sp.*
F 682/2	Mt. Kina Balu, Borneo	Mus. Comp. Zool. Camb. Mass, U. S. A.	2 specimens.
F 681/2	Do. . .	Do. . .	9 specimens.
F 680/2	Do. . .	Do. . .	4 specimens.

Protomyzon borneensis Hora & Jayaram.

1951. *Protomyzon borneensis*, Hora & Jayaram, *Rec. Ind. Mus.*, **48**, pt. 2, p. 193.

D. 1/6 ; A. 2/4 ; P. 1/22 ; V. 1/8 ; C. 18.

Head 4·5 and depth of body 8 in standard length. Diameter of eye contained 2 times in snout and 1·5 in inter-orbital width. Mouth inferior, lips fleshy, upper lip sharp and angular ; lower lip papillated. Rostral fold produced into small clear fleshy prolongations. Two pairs of rostral and a pair of maxillary barbels. A pair of barbel like prolongations at each corner of mouth. Gill-opening extends to ventral surface for a short distance. Origin of dorsal opposite insertion of pelvics, and is nearer to

base of caudal than to tip of snout. Pectoral 1/22 and pelvic 1/8. Pelvic reaches anal opening but falls short of anal fin. In the axil of the pelvic there is a small rudimentary scaly appendage. Anal reaches caudal base. Caudal emarginate. Body covered with small scales except on head and ventral surface as far back as anal opening. Lateral line incomplete, extending up to above anal fin only.

Locality.—Borneo (Mount Kina Balu).

Type specimen preserved in the collection of the Museum of Comparitive Zoology, Harvard College, Cambridge, Mass., U. S. A.

Progastromyzon Hora and Jayaram.

1951. *Progastromyzon*, Hora & Jayaram, *Rec. Ind. Mus.*, 48, p. 191.

Described recently by Hora & Jayaram (*op. cit.*), this remarkable Gastromyzonid genus shows great similarity to two other Bornean genera, *viz.*, *Neogastromyzon* and *Gastromyzon* in the form of its mouth. To facilitate future reference, a short description of this genus is given below.

Snout broad, rounded, much longer than post-ocular part and provided with small tubercles on dorsal surface. Mouth opening extensive, its gape being more than half width of head. Anterior lip overhung by rostral fold which is notched to accommodate four rostral barbels. One small barbel at each angle of mouth. Lower lip fimbriated. Gill-opening just reaches base of pectoral fin, but does not extend to the ventral surface. Scales small, absent on head and region between and before pectoral fins ventrally. Dorsal commences opposite origin of pelvics. Paired fins are flattened and horizontal. Pectorals begin just behind eye and are provided with 21 branched rays each. Pectorals separated from pelvics by a short distance. Pelvics free from each other, not uniting to form a disc-like structure. Pelvics extend beyond vent. Anal fin reaches base of caudal. Caudal peduncle much longer than deep.

Genotype.—Progastromyzon griswoldi Hora & Jayram.

Distribution.—Borneo (Mount Kina Balu).

Progastromyzon griswoldi Hora & Jayaram.

1951. *Progastromyzon griswoldi*, Hora & Jayaram, *Rec. Ind. Mus.* 48, p. 192.

D. 3/8 ; A. 2/5 ; P. 1/21 ; V. 1/9 ; C. 18 ; L. 1.79 ; L. tr. 9/9.

Head 4·5 and depth of body 6 in standard length. Height of head equal to length of snout. Diameter of eye contained 3 times in snout and 2·5 in inter-orbital space. Origin of dorsal ahead of pelvics, and nearer base of caudal than to tip of snout. Least depth of caudal peduncle about 1·7 in its length.

Locality.—Borneo (Mount Kina Balu).

Neogastromyzon Popta.

1932. *Neogastromyzon*, Hora, *Mem. Ind. Mus.*, 12, p. 319, pl. xi, fig. 11 ; pl. xii, fig. 12.

For the diagnostic characters of this genus reference may be made to the key on page 237. Hora (*op. cit.*) has given a complete description of this genus.

Genotype.—Neogastromyzon nieuwenhuisi Popta.

Distribution.—Borneo (River Howong).

Remarks.—The genus is monotypic. Weber and Beaufort (1916), considered *Neogastromyzon* to be con-generic with *Gastromyzon*. Hora (1932) clarifiied the generic status of *Neogastromyzon* and discussed its relationships to *Gastromyzon*. Recently (1951), in dealing with the independent evolution of the Gastromyzonid fishes in Borneo he has discussed the phylogenetic relationships of *Neogastromyzon* with the other Gastromyzonid genera of Borneo.

Neogastromyzon nieuwenhuisi Popta.

1932. *Neogastromyzon nieuwenhuisi*, Hora, *Mem. Ind. Mus.*, **12**, p. 320, pl. x, fig. 11; pl. xii, fig. 12.

D. 2/7; A. 2/5; P. 1/24; V. 1/17; L. 1·90; L. tr. 21/1/10.

Head 4·5 and depth of body 5 in standard length. Diameter of eye 6·4 in head, and 3 in inter-orbital space. Origin of dorsal behind middle of length.

Locality.—Borneo (River Howong).

Gastromyzon Günther.

1932. *Gastromyzon*, Hora, *Mem. Ind. Mus.*, **12**, p. 321.

For a complete diagnosis of this well known genus reference may be made to Hora (*op. cit.*).

Genotype.—Gastromyzon borneensis Günther.

Distribution.—Borneo.

Gastromyzon borneensis Günther.

1916. *Gastromyzon borneensis*, Weber & Beaufort, *Fish. Indo-Austral. Archip.*, **2**, p. 3, fig. 1.

1932. *Gastromyzon borneensis*, Hora, *Mem. Ind. Mus.*, **12**, p. 322, pl. xii, fig. 13.

1948. *Gastromyzon borneensis*, Ramaswamy, *Proc. Zool. Soc. London*, **118**, p. 515. (Cranial Osteology).

D. 3/8; A. 1/6; P. 1/25-27; V. 1/19-20; L. 1.65; L. tr. 19/1/12.

Head 4·25 in standard and 5·25 in total length. Snout more than half length of head. Depth of body below dorsal about length of snout. Diameter of eye contained 7·5 to 8 in head; 5 in snout and 4 in inter-orbital space. Mouth-opening wide, less than three times in length of head.

Locality.—Borneo.

Gastromyzon borneensis is represented in the collection of the Zoological Survey of India by a fine series of specimens.

Reg. No.	*Locality.*	*Donor of Collector.*	*No. of specimens.*
F 672/2	Mt. Kina Balu, Borneo	Mus. Com. Zool. Camb.	4 specimens.
F 673/2	Do. . .	Do. . .	4 specimens.
F 674/2	Do. . .	Do. . .	14 specimens.
F 675/2	Do. . .	Do. . .	13 specimens.

VIII.—DISTRIBUTION AND EVOLUTION OF THE FISHES OF THE FAMILY HOMALOPTERIDAE.

1. *Distribution and Intra-relationships of the family Homalopteridae.*

The family Homalopteridae, highly specialised as it is, has a fairly wide range of distribution, extending from Peninsular India in the west to Formosa in the north east and the islands of the Malay Archipelago in the south. The preponderance of endemic genera and species in the different geographical units here recognised, is a remarkable feature met with among these fishes, for it indicates rapid evolutionary radiation after isolation. The table on pages 177 to 179 gives the distribution of the Homalopteridae according to politacal, rather than geographical divisions but all the same they seem to be fairly distinct zoogeographical entities as the following analysis of the species shows :

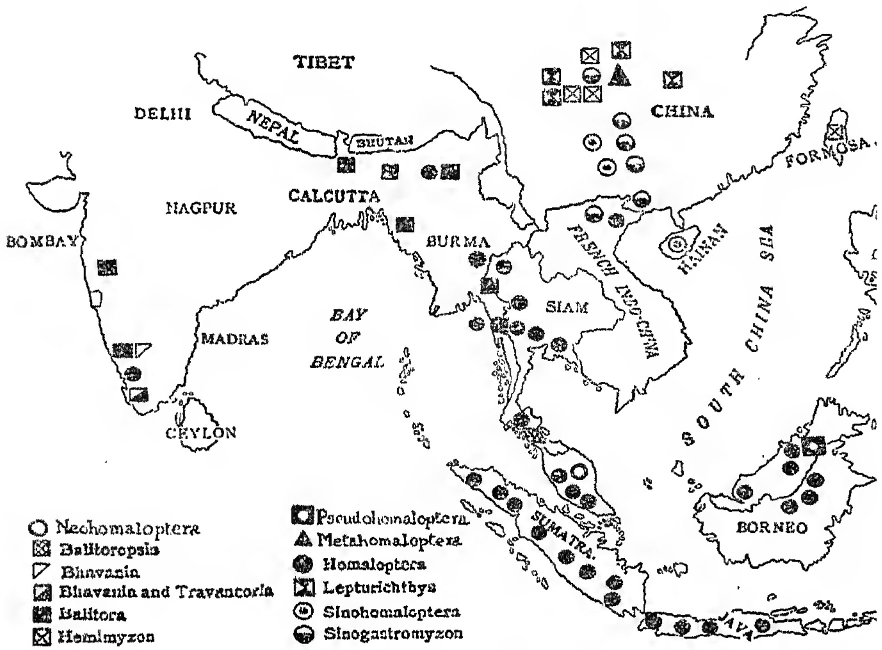
1. *Peninsular India (Western Ghats).*
   - Genus *Homaloptera* van Hasselt.
     - †*Homaloptera montana* Herre.
   - Genus *Balitora* Gray.
     - †*Balitora brucei mysorensis* Hora.
   - †Genus *Bhavania* Hora.
     - †*Bhavania australis* (Jerdon).
   - †Genus *Travancoria* Hora.
     - †*Travancoria jonesi* Hora.
2. *North Eastern India.*
   - Genus *Balitora* Gray.
     - †*Balitora brucei brucei* Gray.
     - †*Balitora maculata Gray.*
3. *Burma.*
   - Genus *Homaloptera* van Hasselt.
     - *Homaloptera modesta* (Vinciguerra).
     - †*Homaloptera bilineata* Blyth.
     - †*Homaloptera rupicola* (Prashad & Mukerji).
   - Genus *Balitora* Gray.
     - †*Balitora brucei burmanicus* Hora.
     - †*Balitora brucei melanosoma* Hora.
4. *Siam.*
   - Genus *Homaloptera* van Hasselt.
     - *Homaloptera modesta* Vinciguerra.
     - *Homaloptera zollingeri* Bleeker.
     - †*Homaloptera lineata* Smith.
     - †*Homaloptera smithi* Hora.
     - †*Homaloptera sexmaculata* Fowler.
   - *Genus *Balitoropsis* Smith.
     - †*Balitoropsis bartschi* Smith.
5. *Malaya Peninsula.*
   - Genus *Homaloptera* van Hasselt.
     - *Homaloptera zollingeri* Bleeker.
     - *Homaloptera wassinki* Bleeker.
     - *Homaloptera orthogoriata* Bleeker.
     - †*Homaloptera leonardi* Hora.
     - †*Homaloptera tweedei* Herre.
   - *Genus *Neohomaloptera* Herre.
     - †*Neohomaloptera johorensis* Herre.

* Indicates endemic genus.
† Indicates endemic species.

6. *Sumatra.*
  - Genus *Homaloptera* van Hasselt.
    - *Homaloptera zollingeri* Bleeker.
    - *Homaloptera wassinki* Bleeker.
    - *Homaloptera ophiolepis* Bleeker.
    - *Homaloptera ocellata* Van der Hoeven.
    - *Homaloptera salusur* Bleeker.
    - †*Homaloptera amphisquamata* Weber & Beaufort.
    - †*Homaloptera heterolepis* Weber & Beaufort.
    - †*Homaloptera gymnogaster* Bleeker.
    - †*Homaloptera modiglianii* Perugia.
    - †*Homaloptera ripleyi* (Fowler).
    - †*Homaloptera ulmeri* Fowler.
    - †*Homaloptera vanderbilti* Fowler.
7. *Java.*
  - Genus *Homaloptera* van Hasselt.
    - *Homaloptera zollingeri* Bleeker.
    - *Homaloptera wassinki* Bleeker.
    - *Homaloptera ophiolepis* Bleeker.
    - *Homaloptera ocellata* Van der Hoeven.
    - *Homaloptera salusur* Bleeker.
8. *Borneo.*
  - Genus *Homaloptera* van Hasselt.
    - *Homaloptera wassinki* Bleeker.
    - *Homaloptera ophiolepis* Bleeker.
    - *Homaloptera orthogoniata* Bleeker
    - †*Homaloptera stephensoni* Hora.
    - †*Homaloptera weberi* Hora.
  - *Genus *Pseudohomaloptera* gen. nov.
    - †*Pseudohomaloptera tateregani* (Popta).
9. *Indo-China.*
  - Genus *Homaloptera* van Hasselt.
    - †*Homaloptera indochinensis* sp. nov.
  - Genus *Sinogastromyzon* Fang.
    - †*Sinogastromyzon tonkinensis* Pellegrin & Fang.
10. *China.*
  - Genus *Sinogastromyzon* Fang.
    - †*Sinogastromyzon hsiashiensis* Fang.
    - †*Sinogastromyzon intermedius* Fang.
    - †*Sinogastromyzon sanhoensis* Fang.
    - †*Sinogastromyzon sichangensis* Chang.
    - †*Sinogastromyzon Szechuanensis* Fang.
    - †*Sinogastromyzon wui* Fang.
  - *Genus *Sinohomaloptera* Fang.
    - †*Sinohomaloptera hoffmanii* Herre.
    - †*Sinohomaloptera kwangeiensis* Fang.
  - *Genus *Hemi nyzon* Regan.
    - †*Hemimyzon abbreviata* (Günther).
    - †*Hemimyzon acuticauda* (Fang.).
    - †*Hemimyzon formosanum* (Boulenger).
    - †*Hemimyzon sinensis* (Sauvage & Dabry).
    - †*Hemimyzon yaotanensis* (Fang.).
  - *Genus *Lepturichthys* Regan.
    - †*Lepturichthys fimbriata* (Günther).
    - †*Lepturichthys güntheri* Hora.
    - †*Lepturichthys nicholsi* Hora.
  - *Genus *Metahomaloptera* Chang.
    - †*Metahomaloptera omeiensis* Chang.

*Indicates endemic genus.
†Indicates endemic species.

From the above analysis of the distribution of species, some very interesting conclusions can be drawn regarding the zoogeography and intra-relationships of the members of the family Homalopteridae. The genus *Homaloptera* has the widest range of distribution, being found in all geographical divisions, except in North Eastern India and in China. Moreover, the species constituting the genus are less specialised than the other Homalopteridae, but at the same time they are highly variable, thus, occupying more or less the central position from which the origin of the other genera could be traced. Both in the Eastern Himalayas and



Text-figure 3 :—Map showing the distribution of the genera of the family Homalopteridae.

in China, the family is represented by highly evolved forms. It is quite likely, that the intense orogenic movements that were prevalent in these places during the later Pliocene and the Pleistocene priods, were directly responsible for the evolution of the highly specialised Homalopterid forms and the elimination of the generalised forms like *Homaloptera* from both these regions. It seems likely, however, that in more secluded positions within these two zoogeographical divisions, *Homaloptera* may have survived and still remains to be discovered. This has happened in the case of the Western Ghats already.

Distributional records and Intra-relationships treated Regionwise.

1. *Peninsular India (Western Ghats)*.—Of the four Homalopterid genera in Peninsular India, the genus *Homaloptera* is represented by one species, while *Balitora* is represented by one variety, both of which are

endemic, though the genera *Homaloptera* and *Balitora* are found in the regions to the east also. Two remaining genera, *Bhavania* and *Travancoria*, which are monotypic, are endemic in Peninsular India. Hora (1944), in propounding his Satpura Hypothesis, referred to the probable source from which the Homalopterid element of Peninsular India was derived. Hora (1950) and Silas (1951) have discussed the Zoogeographical significance of the occurrence of the genus *Homaloptera* and allied genera in Peninsular India.

The genus *Bhavania* and *Travancoria* are *Homaloptera*-like, but have undergone certain specialisations. *Bhavania*, which seems to be an earlier off shoot of *Homaloptera* in Peninsular India, resembles the broad headed *Homaloptera*, but has the gill-openings greatly restricted and at the same time has a rostral groove in front of the mouth overhung by a rostral fold. *Travancoria*, with its more pointed snout, resembles the narrow snouted *Homaloptera*, a relict of which has been recently discovered in Peninsular India in *H. montana*. The gill-openings in *Travancoria*, as also in *Homaloptera*, extend to the ventral surface for some distance, but the development of a rostral groove in front of the mouth, overhung by a rostral fold, is an adaptive specialisation of *Travancoria* not met with in *Homaloptera*. Further, the rostral fold in between the rostral barbels is produced into barbel-like prominences, which indicate an increase in the tactile organs. This by itself is a further specialisation over the *Homaloptera*-type. The tilting of the Western Ghats during the Pleistocene (Menon, 1951), and the consequent rejuvination of numerous torrential streams along the Western Ghats, and the climatic fluctuations during the Pleistocene (Silas, 1952), seem to have provided sufficient impetus for the rapid speciation in the early *Homaloptera* which migrated to the Peninsula from the region of the Eastern Himalayas. *Balitora* of Peninsular India would seem to be a later influx from the North-East.

2. *North Eastern India.*—The areas included in this division are the Eastern Himalayas, including Eastern Nepal and Northern Bengal and Assam. In the region of the Eastern Himalayas, *Homaloptera* under the dynamic changes that took place there as a result of the Himalayan tectonic movements became modified into the narrow snouted *Balitora*-like forms. These subsequently would have migrated to the Western Ghats to the West and the Chittagong Hill tracts and the Arakan Yoma to the South-East and are now represented by *Balitora brucei mysorensis*, *B. brucei burmanicus* and *B. brucei melanosoma*. The stock in the centre seems to have become still further modified and given rise to the broad snouted *B. brucei brucei* and *B. maculata*. As indicated already (*vide supra*,) no species of *Homaloptera* has so far been recorded from this region, but the likelihood of its occurrence there cannot be ruled out.

3. *Burma.*—For convenience, along with Burma, the Chittagong Hill tracts are also included. The genus *Homaloptera* is represented in Burma by three species, of which one, *H. modesta* is also found in Siam. The remaining two species, *H. bilineata* and *H. rupicola* are endemic. Similarly, the two varieties of *Balitora brucei*, *viz.*, *burmanicus* and *melanosoma* are endemic. In possessing a pointed snout and a subcylindrical body, *H. modesta* and *H. bilineata* are less specilised than *H. rupicola*,

a form with a more depressed body and a broadly rounded snout. The circumstances which led to the evolution of the broad headed *Balitora* in the Eastern Himalayas seem to have been responsible for the occurrence of the broad headed species of *Homaloptera* in Northern Burma and the narrow headed forms in Lower Burma. In addition, unlike *H. modesta* and *H. bilineata* the paired fins of *H. rupicola* are more extensive, the pectorals overlapping the pelvics. Recently (Silas, 1951), the relationships of *H. rupicola* to two other species, *H. weberi* of Borneo and *Homaloptera* sp. (*H. indochinensis*, sp. nov.), of Indo-China were discussed and it was pointed out that under similar stresses of enviornmental conditions they seem to have evolved along similar lines , *viz.*, broadly rounded head and extensive and overlapping paired fins.

4. *Siam.*—This division includes both Peninsular and Northern Siam. Of the five species of *Homaloptera* in Siam, two species, *H. modesta* and *H. zollingeri* are non-endemic. *H. zollingeri* is a widely distributed species and has a more or less narrowly pointed snout. The scales are keeled and the pectorals are separated from the pelvics by a considerable distance. The body is more or less subcylindrieal. The above characters and the wide range of distribution of *H. zollingeri* indicates that it is a more primitive form than some of the other endemic species of *Homaloptera*. *H. lineata* and *H. smithi* are more specialised in possessing a broader snout and overlapping paired fins. In the former character *H. sexmaculata* resembles *H. smithi*. The monotypic genus *Balitoropsis* is endemic in Siam, and as stated elsewhere (Silas, 1951), the genus seems to have evolved from primitive *Homaloptera*-like forms in Siam. *Balitoropsis* is not a very highly specialised genus, for it has a subcylindrical form, with a more or less pointed snout, as is seen in *Travancoria* of Peninsular India. The pectorals fall much short of the pelvics. The genus is specialised in the possession of a deep rostral groove in front of the mouth and in the disposition of the barbels.

5. *Malaya Peninsula.*—The family is represented here by two genera, the genus *Homaloptera* being non-endemic and the monotypic genus *Neohomaloptera* being endemic. Of the five species of *Homaloptera* which occur here, *H, zollingeri*, *H. wassinki* and *H. orthogoniata* are non-endemic, while *H. leonardi* and *H. tweedei* are endemic. *H. wassinki* has a wider range of distribution, being also found in Sumatra, Java and Borneo. I have examined a specimen of *H. orthogoniata* collected by Dr. A. W. Herre in Malaya Peninsula, and the species occurs elsewhere in Borneo. *H. leonardi* resembles *H. zollingeri* in certain features. In possessing a broad snout, extensive paired fins (pectorals overlaping the pelvics), and smooth scales, *H. tweedei* seems to be better adapted than the other Malayan species of *Homaloptera*. *Neohomaloptera* resembles the broad headed *Homaloptera*, such as, *H. amphisquamata*, but differs from it in the possession of an additional barbel at the angles of the mouth. Such a condition is seen in *Sinohomaloptera* of China. *Neohomaloptera* would seem to have diverged from the *Homaloptera*-stock in Malaya.

6. *Sumatra.*—Of the twelve species of *Homaloptera* found here, five, *viz.*, *H. zollingeri*, *H. wassinki*, *H. ophiolepis*, *H. ocellata* and *H. salusur* are non-endemic. *H. ophiolepis* like *H. wassinki* is also found in

Java and Borneo, while *H. ocellata* and *H. salusur* are found elsewhere only in Java. The endemic species are *H. amphisquamata*, *H. heterolepis*, *H. gymnogaster*, *H. modiglianii*, *H. ripleyi*, *H. ulmeri* and *H. vanderbilti*. Of these, *H. amphisquamata* is a highly specialised species in which the head and body are greatly depressed and the snout is broad and rounded. Ramaswami (1951) enumerated nine important skull characters by which *H. amphisquamata* could be separated from species of *Homaloptera*, like *zollingeri*, *leonardi* and *rupicola*. According to Fowler (1944), *H. ripleyi* has certain special features, but unfortunately, I have not examined the only known specimen of this species, and so am not in a position to add anything to its known affinities. The relationships of the other species have been discussed already (*vide supra*, p. 245).

7. *Java.*—All five species of *Homaloptera* present here are non-endemic. They are all represented in the fauna of Sumatra, while two species are also found in Borneo.

8. *Borneo.*—The family is represented here by two genera, one of which is endemic. Of the five species of *Homaloptera* in Borneo, *H. wassinki* and *H. ophiolepis* and *H. orthogoniata*, are non-endemic, while *H. stephensoni* and *H. weberi* are endemic. In the last two species the pectorals overlap the pelvics. In addition to a broad snout and an incipient rostral groove, *H. orthogoniata* possesses in each pelvic axil a fleshy appendage, this being another adaptation for life in torrential streams. The last said character is seen well developed in many of the Gastromyzonidae. The genus *Pseudohomaloptera*, is monotypic, and endemic in Borneo. It is characterised by the development of a well defined rostral groove in front of the mouth, extensive paired fins and a narrow elongated caudal peduncle. There is no doubt that *Pseudohomaloptera* has evolved from *Homaloptera*-like forms and has become more specialised than *Homaloptera* along certain lines. The significance of the occurrence of a peculiar Homalopterid in Borneo was discussed recently (Silas, 1951) and it was opined that the form had evolved in Borneo from some primitive Homalopterid stock. Thus Borneo seems to represent a centre of active speciation among torrential fishes. Hora (1951), has also discussed the possibility of the Gastromyzonid fishes in Borneo having evolved there independently under the stresses and strain of environmental factors, from primitive Cobitid stock. The endemic Homalopteridae in Borneo show how rapid divergence could take place from the original stock which should have reached the island before its isolation. The zoogeographical significance of the distribution of the Homalopteridae in the Islands of Malaya Archipelago is dealt with separately.

9. *Indo-China.*—The two non-endemic genera of Homalopteridae *viz.*, *Homaloptera* and *Sinogastromyzon* are represented in Indo-China by one species each. Speaking of the significance of the occurrence of *Homaloptera*sp. (*H. indochinensis*) in Indo-China, it was stated that the form has evolved independently from primitive *Homaloptera*-stock (Silas, 1951). It seems probable that, besides the earlier wave of migration that brought *Homaloptera* to Indo-China, there must have been later and relatively speaking more recent waves which brought a highly

specialised from like *Sinogastromyzon* into Indo-China, for this genus is represented in China by several species. The fish fauna of Indo-China is not well known and so it is not possible to discuss its palaeogeograhy here.

10. *China.*—The Chinese Homalopteridae would seem to have been derived from primitive Homaloptera-stock of which no representative has been found there so far. At present the relationships of the different genera are better known. Of the five genera, four, *viz.*, *Sinohomaloptera*, *Hemimyzon*, *Lepturichthys* and *Metahomaloptera* are endemic, while all six species of *Sinogastromyzon* found there are endemic, though the genus is represented elsewhere in Indo-China also.

Sinohomaloptera is nearest to *Homaloptera*-like forms, and this led (Fang, 1930) to include it first as a subgenus of *Homaloptera*. Later, owing to the structure of the basipterygium, the development of the rostral groove and the presence of one more barbel at each angle of the mouth, it was recognised as a distinct genus. *Hemimyzon* has both broad headed as well as narrow headed forms, as has been described among species of *Balitora*. It has also a very variable caudal peduncle. *Hemimyzon* could perhaps be derived from the broad headed *Homaloptera* species. In *Hemimyzon*, the lips are papillated and the paired fins have convergent bases, both being characters of adaptive significance. *Lepturichthys* seems to be an extreme specialisation of the *Homaloptera*-type which gave rise to *Hemimyzon* forms with narrow heads and elongated caudal peduncle. But it does not lie in the direct line of evolution of *Hemimyzon*. In *Lepturichthys*, a whip-like caudal peduncle is developed. The head and anterior part of the body are greatly depressed. The tactile organs in the form of barbels at the angles of the mouth are well developed and greater in number and the rostral groove is well defined. In addition the lips are papillated and the pectorals nearly reach the pelvics.

From the broad headed *Hemimyzon* type, *Sinogastromyzon* can perhaps be derived. In *Sinogastromyzon* the paired fins are very extensive and the pelvics are united to form a disc-like structure. The body itself is greatly depressed and limpet shaped. Though probably not in the direct line of evolution, but closely related to *Sinogastromyzon* and more specialised than it in some respect, is the genus *Metahomaloptera* of Szechuan in China. *Metahomaloptera*, in addition to possessing united pelvics, has also greatly restricted gill-openings which are situated well above the bases of the pectoral fins. In this respect, *Metahomaloptera* among the Homalopteridae stands in par with *Gastromyzon* among the Gastromyzonidae, and shows parallel development in the reduction of the gill-openings to *Bhavania* of Peninsular India.

2. *Zoogeograpical significance of the distribution of Homalopteridae in the Islands of Malaya Archipelago.*

The fresh water as well as land faunas of the Greater Sunda Islands are so similar to that of Malaya Peninsula, that no doubt can exist about a former union of these islands to the mainland. In addition to geological evidences the faunistic data also throw much light on these former land connections. These islands, situated as they are on the continental shelf,

are surrounded by a shallow sea which nowhere exceeds 100 meters in depth. As a matter of fact, the depth is much less in most places. Hence, during the Pleistocene Glacial periods the portions covered by this shallow sea was a dry land, thus uniting the islands together and they in turn were connected to the mainland. It was Molengraaff and Max Weber (1919), who first drew attention to these Pleistocene land connections, and the continuous land mass was known as the Sundaland. The distribution of the Homalopteridae in Malaya Peninsula and the islands of the Archipelago confirm some of the earlier geological and zoogeographical findings. In addition they also bring to light some interesting aspects of distribution. Before considering these, certain facts of the Paleogeography of the Sundaland are dealt with below.

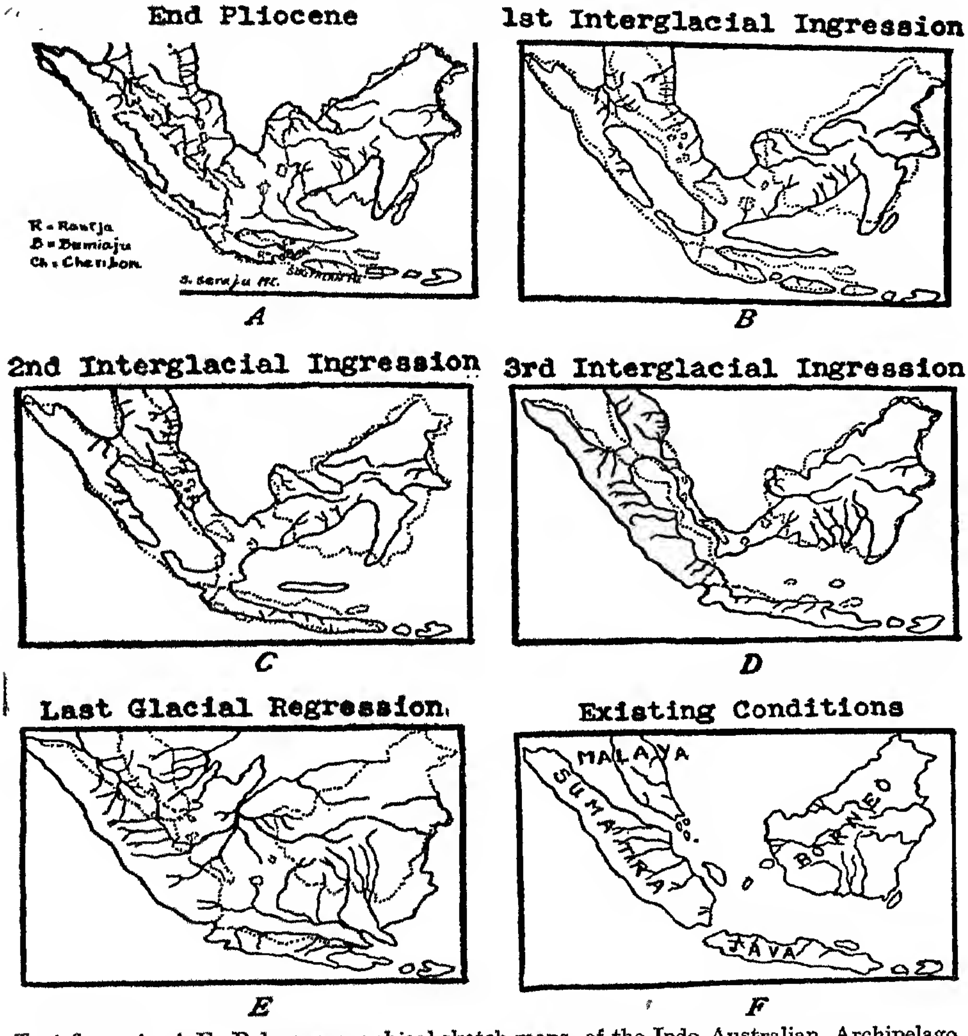
According to Molengraaff (1921), during the glacial times the rivers of Eastern Sumatra and Western Borneo ran through the lowlying plains of the Sundaland which came into existence through the retreat of the sea. These streams ultimately joined into one river which flowed northwards and emptied into the South China Sea. Max Weber, gave zoogeographical support to Molengraaff's view by showing the great similarity of the freshwater fish fauna of the streams of Western Borneo and Eastern Sumatra. The fauna of Eastern Borneo is very peculiar and has very little in common with that of the west.

From former Pleistocene land connections between Java and Borneo relationships in the freshwater fish fauna between Southern Borneo and Northern Java is to be expected. But this is not so, for, their respective faunas are more or less dictinct. Java shows close affinity to Sumatra than to Borneo. Speaking of the Morphological History of the Java Sea, Beaufort (1951), stated :—

> " In the lower Pliocene Western Java formed the end of a Peninsula terminating a land mass which included a great part of Borneo and Sumatra. The rest of Java was mostly below sea, from which only a few smaller islands emerged near its present south coast. During the Pleistocene these islands were joined to Western Java, and only during the third and during the fourth (and last) glaciation was the Java Sea dryland. Then only was direct interchange of faunas between Java and Borneo possible, but even then the watershed running from Sumatra to Borneo and including the islands of Banka and Billiton, prevented the fishes belonging to the 'new invasion' from spreading to the rivers of Southern Borneo and of Java. The land between Java and Borneo may have been low and covered by swamps which may even have been brackish and hence unsuitable for true freshwater fishes."

Further he observed : " According to Smit Sibinga (1947) the Strait of Sunda now separating Java and Sumatra is of very recent origin. To the ancient Chinese it was unknown as a passage for ships. It must certainly be of post-glacial origin. Sumatra and Malaya were still connected at that time. In the time of Ptolemy there still existed a narrow strip of land between them, at a place which is now known as the 'One fathom bank.'"

Maps on the Pleistocene history of the Sundaland based on Glacio-estasism, adapted from Beaufort (1951) are given here, as it is thought, they will help in making clear certain facts about the distribution of the Homalopteridae in the islands of the Archipelago.



Text-figure 4 A-E. Palaeogeographical sketch maps of the Indo-Australian Archipelago based on Glacio-eustasisms (after Beaufort, 1951).

From what has already been said the following important data are deduced :—

1. Pleistocene and recent land connections of the Sundaland with the mainland. These connections were mainly with the Malaya region, and this helped in the spread of Homalopteridae and other freshwater forms to the islands of the Malaya Archipelago.
2. Continuity of the watershed between Western Borneo and Eastern Sumatra.

3. Lowlying and swampy land connections between Borneo and Java preventing dispersal of highly specialised torrential fishes from Northern Java to Borneo or *vice versa*.

4. Last severence of Java from Sumatra during the Holocene.

Let us now consider what light the distribution of the Homalopteridae throw on the above deductions. The family, as already indicated, is essentially a northern element which seems to have originated in South Western China, probably in Yunnan (Hora, 1949), some time during the late Pliocene and reached Malaya Peninsula during the Pleistocene. At none of the stages of the Pleistocene was Borneo separated from Sumatra, nor from Malaya Peninsula, and this is ample evidence to show that the western fauna of Borneo came from this direction. It would seem that from Malaya Peninsula the Homalopteridae migrated to Sumatra and thence through the continuous watershed of the Sundaland to Borneo. Two species of *Homaloptera*, *viz.*, *H. wassinki* and *H. ophiolepis* are common to Sumatra and Borneo. The spread of torrential fishes like *Homaloptera* from Sumatra to Borneo involves a connection between these two places of some altitude, for it is not probable that these fishes could disperse through the lowland rivers. The early homalopterid stock once having reached Borneo would have migrated to their present limits in the island. This west to east influx of Homalopteridae would have been checked as a result of the disappearance of these elevated land connections. These changes did not in any way affect the west to east dispersal of the lowland fishes which are today found common to both these islands.

All through the Pleistocene, Western Java was continuous with Sumatra and species of *Homaloptera*, such as *H. zollingeri*, *H. wassinki*, *H. ophiolepis*, *H. ocellata* and *H. salusur* migrated further south and reached Java. From distributional data, it would seem that *H. zollingeri* and *H. wassinki* were among the earliest to reach Java as they have a wider distribution *H. ophiolepis* would have reached Java prior to *H. ocellata* and *H. salusur*, for it is also found in Borneo. The crustal upheavels of the southern continuation of the direct Himalayan movement in the form of the Malayan Arc passing through Sumatra and Java to further east, would have considerably facilitated the migration of torrential fishes like *Homaloptera* from Sumatra to Java. Later the disruption of land connections between Sumatra and Java during the Holocene, checked further dispersal of the torrential forms from the former to the latter.

Among *Homaloptera*, Java has no species in common with Borneo which does not occur in Sumatra also. This indicates that the Javan and Bornean element of *Homaloptera* were derived from Sumatra. Strangely enough P. and F. Sarasin (1901) also came to a similar conclusion from a study of the land molluscs of these islands. So far as land molluscs go, Java has no species in common with Borneo which does not occur in Sumatra also, and this led them to conclude that Java got its land molluscan fauna from Sumatra and not from Borneo. This molluscan colonization of Java from Sumatra should have taken place during the Pleistocene

glacial epochs, in which case it was also contemporaneous with the dispersal of *Homaloptera* in these islands. The swampy lowlying connections between Northern Java and Southern Borneo were definite barriers to the dispersal of *Homaloptera* from Java to Borneo or *vice versa*. Thus in Java, *Homaloptera* reached a ' blind alley ', in its distribution. From the non-endemicity of *Homaloptera* in Java, it would seem that they are more recent isolates there. It also suggests that, both Borneo and Sumatra were subjected to more intense orogenie movements which indirectly aided rapid divergence of species.

The subsequent severence of land connections of the Sundaland with the mainland and the ingression of the sea resulting in the formation of the large Sunda Islands of Sumatra, Java and Borneo totally isolated the freshwater faunas in these islands. As already indicated, the unsettled orogenic conditions coupled with factors of a torrential environment were of sufficient importance in bringing about rapid divergence in the Homalopteridae in Sumatra and Borneo and also in the other geographical divisions. The great endemicity of these forms indicate that in each geographical division species have evolved within a relatively shorter time.

3.—*Probable lines of evolution of the family Homalopteridae.*

Though it is now known that the Homalopteridae are evolved from Cyprinid ancestors, it has not been possible so far to trace its ancestory to any particular Cyprinid genus or genera. In dealing with the distribution of the family region by region (*vide supra*), remarks were made on the inter-relationships of the species and genera in the different geographical divisions. The recent advances in our knowledge of these fishes has helped to fill in much of the gap that once existed between the different genera. An assessment of their characters reveal that habitudinal variations have brought about repeated divergences and convergences in the family. The following characters may be said to be of functional evolutionary significane in these fishes :—

1. Greatly depressed head and body.
2. Broad snout.
3. Development of a rostral groove.
4. Restriction of the gill-openings to small openings above base of pectoral fin.
5. Extensive paired fins (pectorals overlapping pelvics).
6. Union of pelvics posteriorly to form a disc-like structure.
7. Development of a whip-like caudal pedunele.
8. Tactile organs : greater number of barbels and papillated or fimbriated lips.
9. Development of skin flap in pelvic axil.
10. Smooth scales.

The general depression of the head and anterior part of the body, the compact arrangement of the bones of the skull, the flattened nature of the basipterygium, the reduction of the air bladder, etc., are character

of primary adaptive significance in all the Homalopteridae. Ramaswami (1951) enumerated four important cranial characters on which all Homalopteridae, having taken to life in the torrential streams generally resemble.

To surmise what has already been said regarding the interrelationship of the genera in the different geographical divisions, it may be stated that the earliest step in the specialisation and evolution of these fishes from the *Homaloptera*-type seems to have been a broadening of the snout and the development of a rostral groove in front of the mouth. The snout from the narrow pointed *Helgia*-type tends to become-broad, as is seen in *Bhavania*. Addition of tactile organs such as, increase in the number of barbels and papillations on the lips, more barbels, etc., are seen in some of the genera. Further divergence from the original type is witnessed in the development of more extensive paired fins as seen in many species of *Homaloptera, Balitora, Hemimyzon, Sinogastromyzon, Metahomaloptera* etc., the reduction of the gill-openings to small openings well above the base of the pectoral fins as in *Bhavania* and *Metahomaloptera* and the elongation of the caudal peduncle to form a powerful whip-like structure as in *Pseudohomaloptera, Lepturichthys* and some species of *Hemimyzon*. In *Sinogastromyzon* and *Metahomaloptera*, the pelvics are united posteriorly to form a disc-like structure. From a study of functional morphological adaptations, *Metahomaloptera* seems to be the most highly evolved from in the family.

IX.—DISTRIBUTION AND EVOLUTION OF THE FISHES OF THE FAMILY GASTROMYZONIDAE.

1. *Distribution of the family Gastromyzonidae.*

Unlike the Homalopteridae, the Gastromyzonidae has a somewhat restricted distribution. From the table given on pages 179 to 180 (*vide supra*), it will be seen that they are confined on the mainland of Asia to Indo-China and China (including Formosa) and elsewhere only on the island of Borneo. Their absence in the regions to the west, *viz.*, in India, Burma, Siam, Malaya Peninsula, Sumatra and Java is noteworthy. As will be seen from the following analysis, all gastromyzonid genera are endemic in the three geographical divisions in which they are found at present :—

1. INDO-CHINA.

*Genus *Annamia* Hora.

(motonypic).

*Genus *Sewellia* Hora.

(monotypic).

2. CHINA AND FORMOSA.

*Genus *Liniparhomaloptera* Fang.

(monotypic).

*Genus *Vanmanenia* Hora.

(2 species).

* Indicates endemic genus.

*Genus *Praeformosania* Fang.
(3 species).

*Genus *Formosania* Oshima.
(monotypic).

*Genus *Crossostoma* Sauvage.
(2 species).

*Genus *Paraprotomyzon* Pell. & Fang.
(monotypic).

*Genus *Pseudogastromyzon* Nichols.
(6 species).

*Genus *Beaufortia* Hora.
(6 species).

3. BORNEO.

*Genus *Glaniopsis* Boulenger.
(monotypic).

*Genus *Parhomaloptera* Vaillant.
(monotypic).

*Genus *Protomyzon* Hora.
(2 species).

*Genus *Progastromyzon* Hora & Jayaram.
(monotypic).

*Genus *Neogastromyzon* Popta.
(monotypic).

*Genus *Gastromyzon* Günther.
(monotypic).

Earlier workers held the view that the Gastromyzonid fishes originated directly in Southern China, from whence they migrated southwards and reached Borneo when former land connections existed. Recently, Beaufort (1951, p. 88), speaking of the inter-relationships and geographical affinities of the Gastromyzoninae of Borneo, observed :—

> " In the mountain torrents of Northern Borneo certain curious fishes are found belonging to the Homalopteridae. Among fishes of this group they have gone farthest in the way of adaptation to life in fast running water, as the whole flat underside, surrounded by much expanded pectoral and pelvic fins, forms a large sucker by which the fish can adhere to stones or rocks. Two genera, *Gastromyzon* and *Negoastromyzon*, are known from Borneo, but closely allied forms are found in the mountain streams of Southern China. They are unknown from Java, Sumatra, Malaya or Siam, and the most probable explanation of their occurrence in Borneo is that they came by a direct route from China. This involved

* Indicates endemic genus.

a connection between Borneo and China of some altitude, for it is not probable that these fishes could disperse through lowland rivers. Nor is it probable that they used the Pleistocene land bridge through the Philippines and Formosa, for in that case we should expect to find Gastromyzoninae in the mountains of these islands. As the two Bornean genera are endemic, it is also improbable that they reached Borneo so late. They seem to belong to an older invasion, and their occurrence in the upper course of the Mahakam is in favour of this view."

Much can also be said in favour of the view that the Gastromyzonidae did not reach Borneo from China. Hora (1951), in a thought-provoking paper on the Gastromyzonid fishes of the mainland of Asia and the island of Borneo, has brought forward evidence to show that the Gastromyzonid element in Borneo was not derived from the Chinese mainland. Instead in both these places they represent products of independent evolution from primitive Cobitid stock. It is also interesting to find that none of the Bornean Gastromyzonid genera are present on the mainland or *vice versa*. Collateral evidence as seen in the distribution of the Homalopteridae and the Glyptosternoid fishes of the family Sisoridae, order Siluroidea (Hora and Silas, 1951), suggest that, geochronologically speaking, the Gastromyzonidae date back not earlier than the later part of the Pliocene or early Pleistocene. That the Pleistocene land bridge between China and Borneo could have helped in their dispersal from the north to the south does not seem likely, for, there seems to have been no land connections of appreciable elevation between Borneo and Indo-China or China during this period. Lowlying land connections could not have facilitated the dispersal of such highly specialised torrential fishes over such a wide distance. The following section on the polyhyletic origin of the family Gastromyzonidae will help to make clear its zoogeography also.

2. *Polyphyletic origin of the family Gastromyzonidae.*

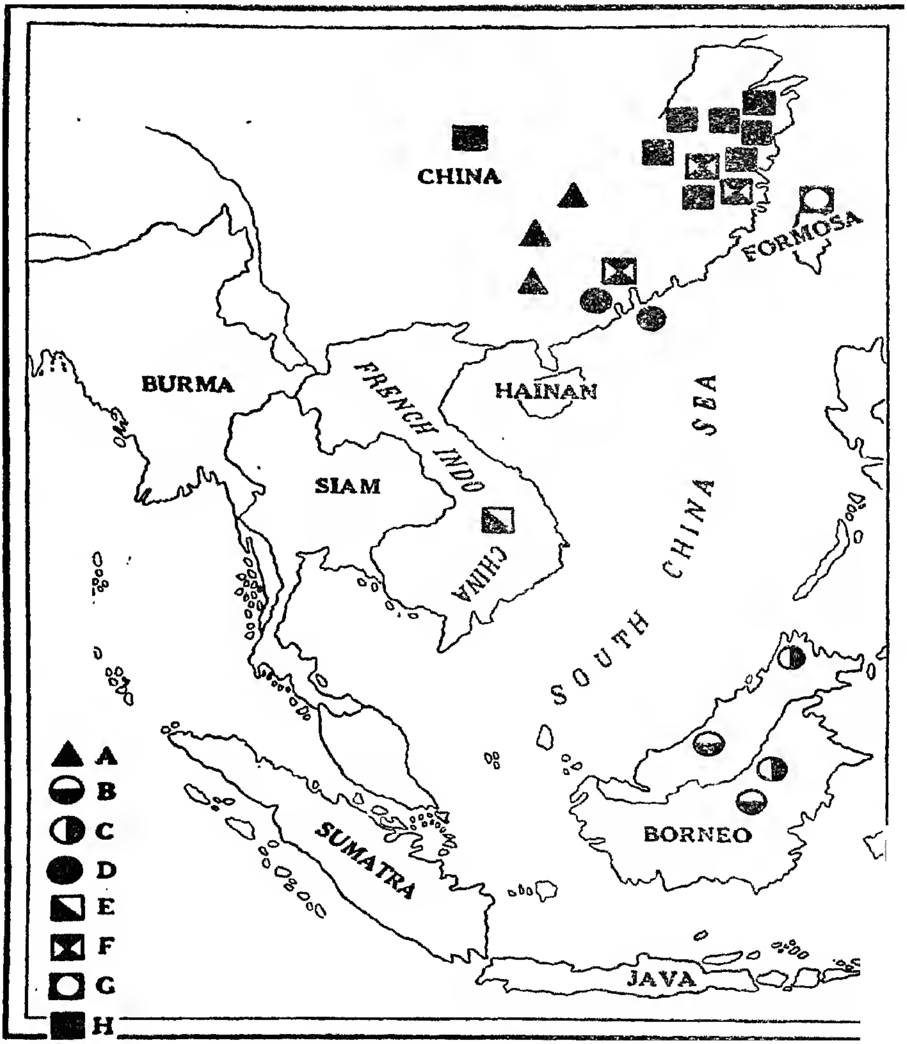
Fang (1935) was the first to draw attention to the fact that the Gastromyzonidae (Gastromyzoninae Hora, 1932) were a polyphyletic assemblage of individuals and divided them into two groups, *viz.*, the Crossostomoid-group and the Gastromyzonid-group. In dealing with the Crossostomoid fishes of China he observed :—

"Crossostomoid fishes are small forms inhabiting the mountain torrents. They are well separated from the Gastromyzonian fishes in having the gill-openings extending to the ventral side of the body and the pectoral fins set immediately behind them."

The Crossostomoid and the Gastromyzonid groups are now recognised as two distinct subfamilies and as already stated, Hora (1951) has discussed the polyphyletic origin of these fishes in the mainland of Asia and in Borneo. His views are elaborated below.

A. Parallel evolution of the Crossostomoid fishes on the mainland of Asia and on Borneo.

Fang (1935) derived the Crossostomoid fishes from a 'Nemachiloid ancestral stock' and regarded them as having evolved independently along three lines, namely, (1) *Annamia* Hora, (2) *Liniparhomaloptera* Fang and *Parhomaloptera* Vaillant and (3) *Vanmanenia* Hora, *Praeformosania* Fang, *Formosania* Oshima and *Crossostoma* Sauvage. Though



Text-figure 5. Map showing the distribution of the fishes of the subfamily Crossostominae.

A.	*Vanmanenia* Hora.	*B.*	*Parhomaloptera* Vaillant.
C.	*Glaniopsis* Boulenger.	*D.*	*Liniparhomaloptera* Fang.
E.	*Annamia* Hora.	*F.*	*Crossostoma* Sauvage.
G.	*Formosania* Oshima,	*H.*	*Praeformosania* Fang.

it is not possible to agree with Fang's views on the inter-relationships of the Crossostominae, one thing is certain, *viz.*, that the Crossostominae by itself is a heterogenous assemblage of independently evolved forms, all, derived from primitive Cobitid stocks, both on the mainland and in Borneo. As such, before dealing with the mainland genera, the evolution of the Bornean genera are dealt with first.

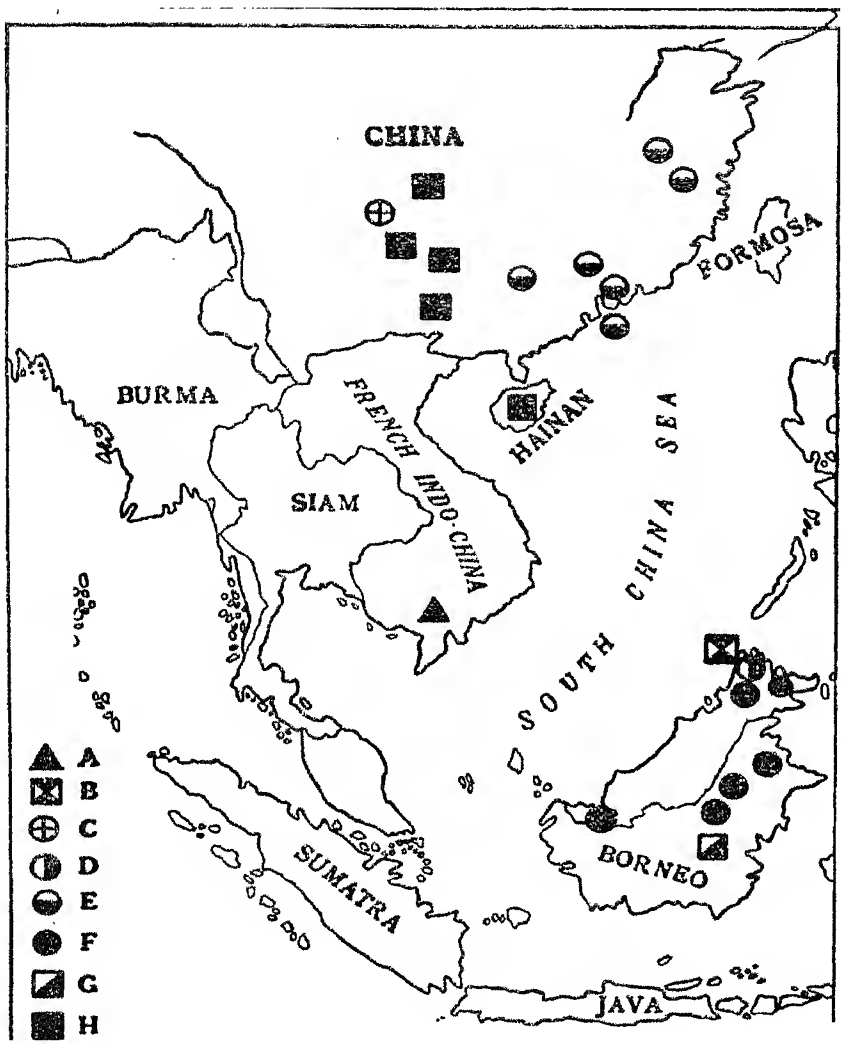
Glaniopsis of Borneo shows a large number of Nemachiline characters, but also exhibits a few important Gastromyzonid features. Ramaswami (1951) has accounted for nine skull characters in which *Glaniopsis* resembles the Nemachiline group, and eight on which it differs from it. According to him, "In possessing independent sensory canal ossicles in the supraorbital, suborbital, temporal and supraoccipital regions and in not having the exoccipital fenestrae, *Glaniopsis* stands apart from the Cobitidae. *Parhomaloptera,* the other Crossostomoid genus found in Borneo, is quite different from *Glaniopsis*, especially in the nature of the mouth and the associated structures. *Parhomaloptera* is more specialised than *Glaniopsis* and it would seem that these two forms have evolved independently in Borneo from primitive *Nemachilus*-like Cobitidae.

On the mainland, the Crossostomoid fishes are represented by six genera, *viz.*, *Vanmanenia*, *Praeformosania*, *Formosania*, *Liniparhomaloptera* and *Crossostoma* in China and *Annamia* in Indo-China. Fang considered *Annamia* and *Liniparhomaloptera* to be independently evolved from 'primitive Crossostomoid fishes'. He was also of the opinion that *Liniparhomaloptera* of China directly gave rise to *Parhomaloptera* of Borneo. But we have already seen that there could have been no interchange of Crossostomoid fishes between Borneo and China or *vice versa*. In the absence of a rostral groove and the disposition of the barbels *Liniparhomaloptera* shows some affinity to *Crossostoma*. It is quite possible that these two forms have been derived from a common ancestral stock, the former being less specialised than the latter, but not in the direct line of evolution of the latter. In addition, *Crossostoma* according to Ramaswami (1951) is characterised by the possession of a pair of prepalatines, a feature which is not found in the other genera studied by him. *Vanmanenia*, *Praeformosania* and *Formosania* represent an evolutionary series of progressive specialisation. Though Fang considered *Crossostoma* as the most specialised of this series, for reasons already indicated, *Crossostoma* is considered to represent an independent line of evolution. *Annamia* of Indo-China, in its slender depressed body, pointed snout, horse-shoe shaped rostral groove, absence of rostral fold, disposition of the rostral barbels and the slender caudal peduncle, is markedly different from the rest of the Crossostomoid fishes, and would seem to represent another independent line of evolution from *Nemachilus*-like primitive Cobitidae.

B. *Parallel evolution of the Gastromyzonid fishes on the mainland of Asia and on Borneo.*

Like the Crossostominae the Gastromyzoninae can be arranged into two geographical units, *viz.*, Pseudogastromyzoni comprising the four genera *Paraprotomyzon* Pellegrin & Fang, *Pseudogastromyzon* Nichols,

Beaufortia Hora and *Sewellia* Hora on the mainland of Asia and the Gastromyzoni including *Protomyzon* Hora, *Progastromyzon* Hora & Jayaram, *Neogastromyzon* Popta and *Gastromyzon* Günther, represented



Text-figure 6. Map showing the distribution of the fishes of the subfamily Gastromyzoninae.

A. *Sewellia* Hora.
B. *Progastromyzon* Hora & Jayaram.
C. *Paraprotomyzon* Pell. & Fang.
D. *Protomyzon* Hora.
E. *Pseudogastromyzon* Nichols.
F. *Gastromyzon* Günther.
G. *Neogastromyzon* Popta.
H. *Beaufortia* Hora.

only in Borneo. These two groups are also separated on definite taxonomical characters, for in the Pseudogastromyzoni (mainland forms) the pectorals overlap the pelvics and the mouths are markedly small being contained less than one-third in the width of the head, while in Gastromyzoni (Bornean forms), the pectorals are separated from the pelvics by a considerable distance, but in *Gastromyzon* and *Neogastromyzon* which are highly specialised genera, lateral flaps of skin are developed to bridge over the space between the paired fins, thus converting the whole ventral surface into an effective suctorial disc. In the extent of the mouth *Progastromyzon*, *Neogastromyzon* and *Gastromyzon* form one group, where it is very extensive and more than half the width of the head. In *Protomyzon* the mouth is about one-third the width of the head. It would thus seem that in Borneo there were two independent lines of evolution among the Gastromyzoni, one giving rise to *Protomyzon* and the other after having evolved to the *Progastromyzon*-stage, diverging along two lines, which are at present represented by *Neogastromyzon* and *Gastromyzon*. Of these *Gastromyzon* seems to be the most specialized genus.

On the mainland *Sewellia* of Indo-China due to its geographical isolation and specialisation appears quite different and independent from the Chinese genera. Likewise *Paraprotomyzon* would also represent another independent line of evolution. The remaining genera, *Pseudogastromyzon* and *Beaufortia*, seem to have evloved from the same stock, but diverged, thus not forming a direct line of progressive specialisation. *Beaufortia* is more highly specialised than *Pseudogastromyzon*, for in it the number of rays in the paired fins are more numerous and the pelvics are united posteriorly to form a disc-like structure.

SUMMARY AND CONCLUSIONS.

It is proposed to present here very briefly the main conclusions reached in the preceding pages. In the present work, a complete revision of the two Cyprinoid families Homalopteridae and Gastromyzonidae is given, with descriptions of a new genus and a new species. From the distribution of these fishes, certain conclusions of zoogeographical significance have been arrived at. In the west, the distribution of the Homalopteridae throws more light on the migration of torrential fishes from the Eastern Himalayas to the Western Ghats of Peninsular India. In the Malaya Archipelago, the Homalopterid element seems to have spread from Malaya to Sumatra and from Malaya and Sumatra to Borneo on the one hand and from Sumatra to Java on the other. There seems to have been no direct dispersal of the highly specialized torrential fishes between Java and Borneo or *vice versa*. The high percentage of endemic species in Sumatra and Borneo and the absence of endemic species in Java suggest that Java received its Homalopterid element more recently. The overlapping distribution of the 'non-endemic' species of *Homaloptera* in the different geographical divisions is noteworthy, and is a clear indication of the north to south trend of dispersal of these fishes.

The study of the evolution and distribution of the family Gastromyzonidae supports Hora's contention (Hora, 1951) that these fishes

have evolved independently in Borneo and on the mainland of Asia from primitive Cobitidae and that the Bornean element thus does not represent forms that had formerly migrated from China directly to the south as was considered by earlier workers. As such, the Gastromyzonidae by itself is polyphyletic the family being divided into two subfamilies, Crossostominae and Gastromyzoninae, the latter being further divided into two divisions, *viz, Pseudogastromyzoni* (on the mainland of Asia) and *Gastromyzoni* (Borneo). As in the case of Gastromyzoninae, the Crossostominae itself warrants a further division on geographical grounds and if proposed should bear the names *Cross ostomini* (on the mainland of Asia) and *Glaniopsini* (Borneo).

Geographical and ecological isolation have thus played a great role in the evolutionary divergence of these fishes. The isolation being complete or almost complete, the divergences have ranged from subspecific, specific and even to generic levels. As environmental factors are equally important in determining the amount of differentiations that have taken place, the effects of the orogenic movements and resulting physiographic changes that greatly affected the drainage systems in South East Asia during the Pleistocene must not be underestimated. These changes must have had profound influence on the speciation and distribution of these fishes. Such changes in the environmental conditions which may be responsible for inducing totally different modifications are also responsible for the high percentage of endemicity seen among the Homolopteridae and Gastromyzonidae.

The repeated divergences and convergences brought about by habitudinal segregation have made it difficult to discern any straight line of evolution in the Homalopteridae and Gastromyzonidae. But all the same, the directiveness of evolutionary trends in them cannot be doubted for, increased specialization is always associated with more efficiency for life in the rapid waters of the torrential streams. Thus in every case, the adaptation met with, relates to a fine adjustment of the animal to the external conditions of its environment. Divergent and convergent evolution, as evidenced from these fishes, indicate more clearly the causes for adaptive modifications, and the utility of such modifications to the organism concerned.

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EXPLANATION OF PLATE V.

Homaloptera montana Herre.

1. Lateral View × 3
2. Ventral View × 3

Neohomaloptera johorensis Herre.

3. Lateral view × 5
4. Ventral view × 5

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THE OCCURRENCE OF *GLOSSOPTERIS* FRONDS IN THE NORTH-EAST FRONTIER TRACTS, WITH A BRIEF REVIEW OF THE GONDWANAS OF NORTH-EASTERN INDIA

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Contents

Introduction

During the field season of 1952-53, two specimens of *Glossopteris* were collected by one of us (T. Banerjee) from certain slaty beds in a road section below Flat Two, in the Sela Sub-Agency, N.-E. Frontier, Assam. The presence of these fronds firmly establishes the Lower Gondwana age of these sediments, and this record now forms the easternmost extent of this genus in the Indian sub-continent. A careful search of these slates (believed to the Damudas), further to the north-east, is likely to yield fruitful results.

Geology

In the submontane tracts of the Assam Himalaya lying immediately to the east of the Bhutan border, a strip of Damuda beds (Permian in age), nearly four miles in width, overlies the Upper Tertiary Tipam rocks in an extensively inverted sequence with the Damudas apparently overlain by the older Dalings to the north. The beds strike parallel to the grain of the hill ranges and, as shown below, extend laterally as a more or less continuous formation along the foot of the Himalaya for considerable distances to the east and to the west, where similar rocks were previously observed by Mallet (1874), La Touche (1885), Pilgrim (1906) and others.

The area from where the fossils were obtained has been examined in recent years. The rocks comprise hard, gray, coarse, and pebbly to medium grained, well cemented, jointed and fractured quartzitic sandstones, inter-stratified with black carbonaceous slaty shales and thin coal seams. The beds have suffered much disturbance and have been somewhat metamorphosed. The sandstone is intimately

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veined with quartz; the coal has been rendered flaky and powdery and the beds sometimes show local acutely overturned folds.

Description of Fossils

Only two specimens were obtained from the slaty shales in the Sela area, of which one is fairly well preserved. The better preserved, but incomplete frond (Figs. 1, 1A), measures about 8·5 cm. in length, and it is at least 3 cm. broad with a clearly marked, comparatively thin, persistent midrib from which bifurcating and freely anastomosing secondary veins arise at acute angles arching slightly outwards a short distance from the midrib. The tip of the leaf is not clearly seen, but it would appear that it was somewhat blunt. The base is not preserved. The secondary veins are numerous, crowded, and more or less parallel with narrow, elongate meshes which are longer near the midrib, but contracting towards the margin.

In our opinion this specimen which is undoubtedly a *Glossopteris,* may be accommodated with some hesitation in the species *Glossopteris indica.* Owing to its fragmentary nature, we are at present inclined to refer it as *Glossopteris* cf. *G. indica.*

The second specimen figured here (Fig. 2) is a rather poorly preserved, comparatively narrow frond about 2·5 cm. broad and more than 10 cm. long. A distinct midrib is present; the anastomosing secondary veins are hardly visible; but there are sufficient indications to justify its inclusion in *Glossopteris,* although specific determination is difficult. It may probably belong to the same species as the one described above.

Beyond indicating that the sediments are undoubtedly Lower Gondwanas, the specimens are not helpful for closer age determination. But the narrow strip of the Gondwanas of the north-east Himalayan foot-hills, stretching more or less continuously from Abor Hills in the east to Nepal, and further to the west, are generally believed to be the Damudas.

Gondwana Sediments in other parts of North-Eastern India

Opportunity is taken to review briefly our knowledge of the known fresh-water Gondwana sediments and the marine intercalations in Assam and the adjoining territories in north-eastern India the distribution of which is of importance in Gondwana palaeogeography.

Darjeeling Area.—At Pankabari, on the Darjeeling Gondwanas, Hooker (1854) and Mallet (1874) reported the occurrence of *Glossopteris* sp., *Vertebraria indica, Phyllotheca* sp. and *Sphenophyllum speciosum.* The Lower Gondwanas in this area are composed mostly of highly disturbed and crushed, grayish, massive-bedded, felspathic, and occasionally calcareous sandstones and sandy micaceous shales which are sometimes carbonaceous with occasional coal seams (Mallet, 1877; Bose, 1890; Ray, 1947). A glacial boulder bed has been reported by Fox (1934, p. 9) and Auden (1935) above Tindharia station occupying a position at the base of the Gondwanas. This discovery, according to Fox (1934, p. 9), has rendered uncertain the correlation of the Darjeeling and the Eastern Himalayan Gondwanas with the Raniganj and he suggests the possibility of the Himalayan Gondwanas belonging to the Barakars. As shown elsewhere in this paper, the question of their age cannot be considered as settled and needs careful re-examination.

Sediments believed to be the Damudas have been recognized in a narrow, more or less continuous belt further to the east of Darjeeling up to the region of the Abor Hills; but till now undoubted plant fossils have not been found in these sediments. The present discovery is therefore of some significance.

Sikkim.—Quite recently G. N. Dutt and S. N. Sen of the Geological Survey of India, located plant-bearing Gondwana beds in the Rangit valley in Western Sikkim,

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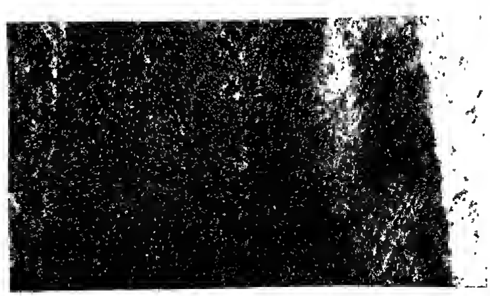
1



1A × 2

FIG. 1. *Glossopteris* cf. *G. indica*. × Nat. size.
FIG. 1A. *Glossopteris* cf. *G. indica*. Same specimen as above, enlarged to show venation. × 2.
FIG. 2. *Glossopteris* sp. A poorly preserved specimen, probably belonging to the same species as the one figured above. × Nat. size.

The specimens are preserved in the Museum of the Geological Survey of India.

situated some distance to the north of the fossil locality Pankabari in the Darjeeling area. The poorly preserved plant remains were collected by Dutt from a locality about two miles west of Asangthang from slightly altered sandstones a few hundred feet above certain 'pebble beds' (believed to be the equivalents of the Talchir boulder bed) which, apparently, occupy a basal position in the series and are well developed near Khandosangphu and Khemgaon. The plants include *Schizoneura, Vertebraria indica* and a doubtful *Glossopteris* (? *Gangamopteris*). Sen's specimens come from a locality about two miles north-east of the junction of the Rangit and the Roathak Khola, north of Naya Bazar, and include an imperfect specimen of *Glossopteris*, probably *G. indica*. These recent fossil finds in Western Sikkim conclusively prove that this series of sediments (at one time thought to be a part of the Dalings), occurring isolated from the Gondwana exposures of the southern foot-hills of the Darjeeling Himalaya, is also undoubtedly Lower Gondwana.

The Gondwanas are particularly well exposed in the form of a 'window' in the Rangit valley, 12 miles north of Darjeeling (Ghosh, 1952, 1953) and contain a few thin seams of semi-anthracitic coal (see also La Touche, 1910; Mallet, 1874). The sediments which have been traced for about 14 miles along the bridle path from Naya Bazar nearly to the base of the descent from Rinchinpong, consist mainly of grey, gritty and felspathic sandstones and carbonaceous slates 'and have at their base tillite and varved slates.....' (Ghosh, 1952). The tillite recalls the glacial boulder bed of the Himalayan foot-hills reported by Fox (1934, p. 9) and Auden (1935) at Tindharia, in the Darjeeling foot-hills, and the pebble beds noticed at the base of the Gondwanas in the Lish valley south of Kalimpong, the Balipara frontier area, the Abor Hills and in the Kosi valley in Nepal. The Lachi pebble bed of North Sikkim mentioned below may also represent a contemporaneous stratigraphical horizon of glacial origin.

North of Namchi near Khemgaon in W. Sikkim, A. M. N. Ghosh (1952, 1953) and T. Banerjee found *Spirifer* (? *Neospirifer* cf. *moosakhailensis*) and fragments of other 'Permo-Carboniferous' marine brachiopods and bivalves in a loose block. G. N. Dutt informs us that he re-visited the area and located the source bed of the fossiliferous rocks, and in exposures of these marine beds between the Tista and the Rangit rivers, he collected many more fossils including, species of *Spirifer* (? *Neospirifer*), *Productus*, *Fenestella* (? *Fenestrellina*), etc.

Wager (1939) collected Carboniferous and Permian marine shells from the Lachi ridge in N. Sikkim. Based on the study of these fossils Muir-Wood and Oakley (1941) have recognised two fossiliferous horizons, namely, a Middle or Upper Carboniferous consisting of limestones and shales and an Upper Permian * mostly of sandstones. The former contain *Productus* sp., *Athyris* sp., *Spirigerella* sp., *Straparollus* sp., and *Ellipsellipsopa* sp. In the Upper Permian horizon of fossiliferous sandstones were recognised *Waagenoconcha purdoni* (Dav.), *Camarotaechia* sp., *Uncinunellina jabiensis* (Waag.), *Syringothyris lydekkeri* (Dien.), *Batostomella* sp., *Fenestrellina* aff. *fossula* (Lons.), *Nuculana* sp., *Parallelodon* aff. *tenuistriatum* (Meek and Worthen), *Pleurophorus* sp., *Aviculopecten hyemalis* (Salt.), *A.* aff. *leniusculus* (Dana) and *Pleurotomaria* aff. *orientalis* (Roem.). Between these two fossiliferous horizons occur certain 'pebble beds' about 600 ft. in thickness. The 'pebble bed' is a grit composed of ungraded angular quartz grains and felspar set in a very fine paste of quartz and mica with sparsely scattered pebbles consisting of dark quartzites and pinkish limestone. The beds are suspected to be the equivalents of the uppermost Carboniferous Talchir boulder bed of the Peninsula and the Blaini boulder bed of the Simla region (Muir-Wood and Oakley, 1941; Auden, 1935).

There is also a slightly higher horizon in the sandstones overlying the 'pebble beds', containing Orthotetid, *Chonetes wageri* Muir-Wood, *Dictyoclostus* cf. *gratiosus* (Waag.), *D.* cf. *subcostatus* (Waag.), *Linoproductus* cf. *cora* (d'Orb.), *Marginifera*

* The possibility of this horizon being Lower Permian should also be borne in mind.

himalayensis Dien., *Pustula* sp., *Neospirifer moosakhailensis* (Dav.), *Spiriferella rajah* (Salter), *Goniocladia* sp. and *Rhombopora* cf. *circumcincta* Reed.

According to Muir-Wood and Oakley (1941, p. 66) the two upper Lachi fossil beds overlying the glacial 'pebble beds' are of 'Upper Permian, Kazanian age (= Productus shales and Zewan beds)'. The underlying lower fossiliferous bed, in their view, would be Middle or Upper Carboniferous and may belong to the Mount Everest Limestone. The Lower Permian is probably missing in this sequence.

Subansiri Gorge.—The above occurrences of marine fossils at the base of the Gondwana in Sikkim recalls Maclaren's (1904) find of boulders of fossiliferous Permo-Carboniferous limestone at the mouth of the Subansiri gorge about 350 miles to the west of the above locality. About 20 boulders and pebbles of fossiliferous limestone, some arenaceous and the others argillaceous, were picked up by him, and these revealed the following genera and species (Diener, 1905):—from the arenaceous limestone boulders: *Productus* cf. *pustulosus* Phill., *Spirifer* sp., *Spiriferina* sp., *Reticularia* cf. *inaequilateralis* Gemm., *Dielasma* aff. *uralica* Krot., *D.* aff. *biflex* Waag., *Dielasma* sp.; from the hard, bluish argillaceous limestone boulders: *Chonetes* cf. *carbonifera* Keys., *Mylina* sp., *Monopteria subansirica* Dien., *Laxonema* sp., *Pleurotomaria* aff., *punjabica* Waag., *Bellerophon* sp., *Fenestella* sp. and impressions of Crinoidea. According to Diener these fossils recall the Kuling shales of Lilang and Spiti which are generally rich in *Chonetes carbonifera*. Maclaren correlated this horizon with the Lower Productus limestone of the Salt Range and suggested a close connection with similar beds in Spiti and China, and 'possibly of Tenasserim and Southern Shan States'. Muir-Wood and Oakley (1941), however, correlate the fauna with that of the Upper Productus limestone. The correct horizon needs future verification.

Although the specimens were not obtained from beds *in situ*, there is not much doubt, 'from the lithological characters of the boulders, that they could not have travelled for any great distances' (Holland, 1905). Maclaren (1904) himself suggested that the locus may possibly be looked for at the base of the Damuda series 'at no very great distance from the Assam plain'. Alternatively, he suggested that the original beds might occur at the edge of the Tibetan plateau. But from the nature of the boulders which we have examined, it appears to us that the first suggestion is more plausible. In recent years B. Laskar of the Geological Survey of India again found two or three boulders from the Subansiri, composed of hard, bluish, argillaceous limestone in which the only fossil identifiable was a poorly preserved *Chonetes* cf. *carbonifera* Keys. It is, therefore, of prime importance to search for the original beds from which these boulders have been derived, most probably at no great distance from the belt of Tertiary sediments.*

Abor Hills.—Rolled limestone boulders which are slightly arenaceous containing badly preserved crinoid ossicles have also been reported in the upper course of the Sireng river in the Abor Hills (Coggin Brown, 1912). 'These rocks undoubtedly belong to the base of the Gondwana series, and must occur somewhere in the steep jungle-covered ravine slopes of the upper Sireng' (Coggin Brown, 1912). According to Muir-Wood and Oakley (1941, p. 60) the Subansiri fauna and the Abor Hills marine limestone boulders with the poorly preserved fossils providing very meagre data for correlation, may be of the same age as the upper Lachi fossil horizons overlying the glacial 'pebble beds'. The fossiliferous beds of the Rangit-Tista area in south-western Sikkim may also be of the same age (Upper Permian).

With regard to the fresh-water sediments in the Abor Hills, near Rammidumbang contorted black carbonaceous shales (coaly in places), believed to belong to the Lower

* Early in 1953, Laskar again visited the area and he informs us that he located the bed composed of the hard, bluish, fossiliferous limestone in the Ranganadi basin, about 20 miles south-west of the Subansiri (Maclaren's locality) and only a few hundred feet from the Tertiary belt lying to the south.

Gondwana, have been recognised. Hard, white sandstones, contorted grey slates and reddish brown shales are well exposed in the Sirpu stream. There are also quartzites, carbonaceous shales interbedded with quartzites, and a 4′-5′ thick coal seam. Gondwanas are also exposed in the upper Sireng valley to the south-west of Kalak where sandstones and shales are prominent.

Bhutan.—In Bhutan (Pilgrim, 1906; 1906*a*) the Gondwanas are well exposed in the Kala Pani where soft sandstones interbedded with crushed coal seams occur. The upper bands of sandstone are quartzitie with thin intercalations of carbonaceous shales. Similar sediments also occur in the Bor Naddi, 12 miles to the west and in the Nunai Naddi, four miles to the east.

Aka Hills.—La Touche (1885) recognised Lower Gondwana sediments in the Aka Hills in the Lower Himalaya to the north of Tezpur in Assam. The geological features are similar to those of the Gondwanas in Sikkim to the west and the Daphla to the east.

In the upper waters of the Bhareli river, Damuda rocks are found as narrow contorted bands of hard quartzitic sandstones interstratified with carbonaceous shales and seams of coal, dipping at high angles to the south.

Dikrang Valley.—Further east on the Dikrang river, south-west of the Subansiri and the Ranganadi, are found clay shales, often carbonaceous and interstratified with thin bands of sandstone. The carbonaceous shales occasionally pass into a crushed splintery coal.*

Garo Hills and ?Tripura.—The only other undoubted occurrence of Lower Gondwana sediments in the north-eastern parts of India, is in the western extremity of the Garo Hills at Singrimari where Fox (1934, p. 29) discovered a small patch of carbonaceous shales containing specimens of *Vertebraria indica.*

In 1952, S. N. Sen of the Geological Survey of India handed over two specimens of plant impressions on carbonaceous shales from Tripura State which proved to be *Vertebraria indica.* But the true provenance of these undoubted *Vertebraria* requires confirmation before anything further could be stated on the significance of the occurrence of Gondwana sediments so far east in a major basin of Tertiary sediments.

Conclusions

The distribution of the fresh-water Gondwana sediments with the marine Permo-Carboniferous deposits at the base in the eastern Himalayan region, although still not fully known, gives us some idea of the trend of the northern coast line of Gondwanaland. Holland (1905, p. 135) expressed the opinion that 'the Crystalline axis of the Himalayas has been a long persistent land-mark in the physical history of Central Asia, marking approximately the northern boundary line of the great Gondwana continent, and forming the southern shore of the . . . Tethys'. While it may be partly true, it should be remembered that the 'Crystalline axis' or the 'Central gneiss' of the Himalaya, is apparently a mixture of rocks of different ages, mainly granitic in composition, some of them pre-Tertiary and some Tertiary in age.

In the Lachi area in North Sikkim, as shown above, there was a marine phase in the Middle or Upper Carboniferous times. This sea did not apparently reach the Darjeeling-Subansiri-Abor Hills region in the Himalayan foot-hills. But it should be remembered that we have as yet no satisfactory data available indicating the definite age of the Dalings or the Baxas. Parts of the Carboniferous might be represented by the former. But it is not unreasonable to hope for future dis-

* The marine fossiliferous band recently located by B. Laskar in the Ranganadi (verbal communication), may most probably extend south-eastwards in the vicinity of the Dikrang valley and should also be searched further south-westwards at the base of the Gondwanas. It is most likely that this marine band may be traced from Abor Hills (where fossiliferous limestone boulders have been found in the upper Sireng valley), to the Dikrang and perhaps even further westwards along the foot-hills within a short distance of the Tertiary sediments.

coveries of organic remains which may throw considerable light on the age and the palaeogeography of these regions.

The later retreat of the Middle or Upper Carboniferous sea northwards was followed by the spread of ice-sheets during the uppermost Carboniferous. The extension of the Gondwana ice-sheet from the south as far north as, and probably beyond, Lachi is suggested by the glacial bed ('pebble bed') in northern Sikkim. The tillites with varved slates in Western Sikkim (Ghosh, 1952) clearly suggest glacial conditions on land, for varved clays are seldom, if at all, formed by the action of ice drifting into shallow seas from glaciated continental margin. It would therefore appear that Gondwanaland extended over most of Nepal, Sikkim, Bhutan and to the north of the Dafla and Abor Hills. If we accept the views of Muir-Wood and Oakley, the Lower Permian in the north-eastern parts of India is apparently not represented due to non-deposition, unless, of course, parts of the Baxas are proved to occupy that position. During the Upper Permian, shallow marine conditions again prevailed in most parts of Sikkim extending westward to Kumaon, Garhwal and Kashmir, and eastward up to the Subansiri river and Abor Hills regions lying to the south of the 'Crystalline complex'.

It is possible, as Fox (1934, p. ii) has stated, that the Gondwana sediments were deposited widely over north-western Assam and north-eastern Bengal as part of the Damudas of the Bengal and Bihar coalfields, and the present discontinuity is due to 'dislocations by faulting and mountain uplift and to enormous erosions of exposed surfaces since the close of the Palaeozoic era'. 'Furthermore, there are now cogent reasons for believing that a line of faulting trends up the Brahmaputra side of the alluvium from the delta above Barisal NNW into Cooch Behar towards the western border of Bhutan. The upthrow side of the fault is the Garo Hills of Assam (where a small patch of Lower Gondwana sediments is seen in the western extremity), so that the movements tend to drop the coal measures, if any (between the Garo Hills and the Bengal-Bihar coal measures) deeper under the alluvium' (Fox, 1934, p. 30). Mallet (1874, pp. 32-33) has also suggested that the coal-bearing Damudas may underlie the alluvium between the Darjeeling Himalaya and the Rajmahal Hills. In the Brahmaputra Valley, in northern Assam, the evidence of gneissic inliers and other factors suggests probable severe overthrusting in the Himalayan region and extensive erosion of the areas to the south of it before the Gangetic alluvium was laid down, so that except close to the Himalayan foot-hills in the valley where the thickness of the alluvium is likely to be great, the Gondwanas are not likely to be present.

The Gondwana sediments in Sikkim and the southern foot-hills of the Himalaya, as mentioned above, are believed by some to be Upper Permian, probably representing the upper part of the Damudas; but *Glossopteris* and certain other elements of the Gondwana flora (*Noeggerathiopsis hislopi*, *Palaeovittaria kurzi*, etc.) have been reported to occur in younger rocks (? Rhaetic) in Tongkin beyond the Shan States (Zeiller, 1903), and if this is correct their likely path of eastward migration across the marine barrier of the Tethys at some period before the end of the Triassic, probably by means of a land-bridge or an island chain, might have lain in the north-eastern parts of Assam, possibly in the vicinity of the north-eastern syntaxis and the adjoining territories to the north. Jongmans (1937, 1937*a*), Sahni (1938), Halle, Just (1952) and some others, however, believe that Zeiller's *Glossopteris* from Tonkin may not be true *Glossopteris* and that the southern flora never invaded the Cathaysia flora (see also Holland, 1943-44). Nevertheless, some minor resemblances are there which demand an explanation. Detailed field investigations in the difficult parts of the country in N.E. India may throw some light on this aspect of Gondwana palaeogeography, in addition to bringing to light a more representative fossil flora from that region which may show the presence of eastern elements as well.

In this connection the discovery by Fox (1931, p. ii) in the lower Barakars (Lower Permian) of the Jharia coalfield, of calamitean shoots which are closely

related to, if not identical with *Lobatannularia* sp. (Kawasaki, 1927; Halle, 1927; Seward, 1931, pp. 235, 236) characteristic of the Lower Permian Shansi flora of China (Upper Shihhotse series), is of considerable interest. The Shansi flora, as in the case of the Russian Kusnezk flora both of which are essentially Permian, shows a large number of plants of Mesozoic type, and *Lobatannularia*, among others in the Shansi flora, is of further significance as forming a connecting link, according to Seward (1931, p. 329), between the Palaeozoic and the Mesozoic floras.

The Indian specimens occur in the floor shales of the IX seam near Barwabera. This solitary report which has nearly been lost sight of in a large memoir by Fox (1931), requires emphasis and a detailed illustrated account of these interesting specimens is now under preparation by the senior author, who has recently re-examined the specimens. Although this form is very poorly represented at the only locality known in India and no other forms characteristic of the eastern Permian flora have been found so far, it will, nevertheless, be unwise not to bear in mind the possibility of intermigration between the Chinese Shansi flora (Gigantopteris flora) and the Indian Gondwana flora across the marine barrier. Evidence at present available is no doubt too meagre to draw far reaching conclusions. It is all the more important, therefore, to search for possible traces of the eastern Shansi flora in the Gondwana sediments particularly of the north-eastern parts of India which probably lay in the path of migration. Hsü (1952, p. 260) considers it hardly possible that there was an early Permian land connection between Gondwanaland and Cathaysia, but the possibility of such a connection should not be easily discarded on grounds which are not entirely convincing.

A noteworthy feature of the generally metamorphosed Gondwana sediments of the Himalayan region in North-East India, is the rarity of fossil finds. While a careful search may bring to light megafossil impressions in more satisfactory numbers, it is most unlikely that microfossils like spores may be met with in altered sediments, as these microscopic remnants of actual cutinous vegetable substance (and not impressions or casts) are usually destroyed by metamorphism because they are generally smaller than the average size of the newly formed minerals and have a tendency to volatilise easily during the process of sediment alteration. Numerous samples of somewhat metamorphosed Gondwana rocks including coal have been examined in the Survey laboratories during the past few years without satisfactory results. But we could certainly expect future finds of megafossils in the Himalayan Gondwanas which were deposited in the marginal areas of the ancient continent and have not suffered a high metamorphism.

Digressing from the main topic of this paper, it is suggested that search should also be made for traces of organic matter (*a*) in the metamorphosed Dalings (Nepal, Sikkim and Darjeeling areas), consisting predominantly of slates and phyllites passing into mica-schists where they merge with the Darjeeling gneiss; (*b*) the Baxas (Bhutan area), mostly composed of slates, phyllites, quartzites, mica-schists, limestones and dolomites; (*c*) and other argillaceous schists and gneisses of the Himalayan region in the north-eastern parts of India, where they all apparently overlie the Gondwanas in inverted sequence. Although their respective ages have not been proved, it has been suggested by Wager (1939) that the Dalings, once a thick dominantly argillaceous deposit, now largely chlorite schists, may be Carboniferous or somewhat earlier in age, while the Baxas may represent metamorphosed ?(Permo-) Carboniferous sediments.

We may also recall the independent suggestion put forward by Auden, and Heron (Auden, 1935, p. 162) that 'the pelitic component of the Darjeeling gneiss may be the same as the Daling series ... If the above correlations are correct this would mean that the sedimentary part of Darjeeling gneiss is the same as the Mount Everest pelitic series' (Carboniferous or somewhat earlier) (Wager, 1939, p. 186). Ray (1935, pp. 29, 41, 44; 1947) also thinks that the Darjeeling gneiss and the Daling series may represent different metamorphic facies of one continuous

sedimentary succession, and suggests the 'increasing possibility' of the Dalings and the Darjeeling gneiss being Palaeozoic. That the Gondwanas and the Dalings may perhaps be considered as constituting one continuous formation showing different grades of metamorphism is also suspected by him (Ray, 1947, p. 118). This suggestion has been questioned by Ghosh (1952, p. 197). However, it should be remembered that some of the sediments in Western Sikkim previously referred to the Daling series, have now been proved to be Gondwanas.

However shapeless one's present ideas may be on the age of the Dalings and the Baxas, the important point is to remember that organic remains have been found in the past in highly altered Palaeozoic and later sediments, and if Wager's suggestion as to the age of the above series is anywhere near the truth, a serious search for fossils in the metamorphic rocks of the Himalaya should be made which, if successful, may help to fix their age with a greater degree of certainty, and will go a long way in understanding more fully the processes of metamorphism and the nature of deformation in the region of metamorphism in orogenic belts. It may be of interest to recall that fossils such as the ammonite *Ariatites* have been known to occur in zoisite-biotite-schist (Liassic Bündner Schiefer, Switzerland), the lamellibranch *Gryphea* in marble (Bündner Schiefer), the anthozoans *Halysites* and *Favosites* in marble (Silurian, New Hampshire), the lamellibranch *Cardinia* in zoisite-garnet-mica-schist (Bündner Schiefer), the brachiopod *Spirifer* in quartz-plagioclase-garnet-biotite-gneiss (Silurian, New Hampshire), the lamellibranch *Halobia* in solid garnet rock (Triassic, Navada), etc. (Bucher, 1953).

As Bucher (1953, p. 292) explains the preservation of fossils in such highly altered sediments, '... typical metamorphic rocks, such as chlorite and mica schists, can form as a result of re-crystallization alone, with or without introduction of atoms or ions, in the presence of pressure differences that give direction to crystal growth, but need not produce differential movements. This does not mean that in many, perhaps most, cases mechanical effects did not play a rôle also, at least on the microscopic scale. But they are incidental, not essential to the production of schistosity in metamorphism. That is why fossils are not destroyed by metamorphism, provided they are much larger than the average size of the newly formed minerals.'

As regards the Dalings and the Baxas, however, the possibility should be borne in mind that parts of these were originally sediments which occupied the deeper parts of the Himalayan geosyncline, and generally benthonic fossils are found to be rare in such sediments. 'A careful analysis, ... leaves little doubt that, of all possible factors, considerable depth of water is the one that will reduce the benthonic fauna drastically, no matter what sediment accumulates on the sea floor.' In such areas a marine depression of sufficient depth was produced to prevent the occupation by a normal benthonic fauna. This aspect has also been discussed in some detail by one of us (Jacob, *in the press*) in a paper on the radiolarian cherts found associated with ultramafics in the Andaman geosynclinal belt. However, attempts should be made to look for fossils in the metamorphosed sediments in the Himalaya which, at first appearance, may be most unpromising. The extreme hardness of these rocks which prevents easy accessibility to the usually poorly preserved and comparatively rare fossils in them and the general unpreparedness to expect remains in highly metamorphosed rocks, might have contributed, in part, to the scarcity of fossil finds in them.

We are grateful to Dr. M. S. Krishnan, Director, Geological Survey of India, for his valuable suggestions.

Summary

In this paper is described a few fronds of *Glossopteris* recently found in the Sela Sub-Agency in the North-East Frontier tracts of Assam. The discovery conclusively proves that the fresh-water sediments which yielded these fossils undoubtedly belong to the Lower Gondwana. These sediments run in a more or less continuous belt along the foot-hills of the Himalaya from Nepal

to tho Abor Hills in tho east. *Glossopteris* and certain other genera were previously known from the Darjeeling aroa and the present record now forms the easternmost extent of this flora in tho Indian sub-continent.

Our knowledge of the known fresh-water Gondwana sediments, and the marine intercalations, in Assam and the adjoining territories in north-eastern India, of importance in Gondwana palaeogeography, is also reviewed. The recent finds of *Glossopteris, Schizoneura* and *Vertebraria* and an underlying marine Permian in the Rangit valley in Western Sikkim, and the location of a dofinite fossiliferous Permian bed in the Subansiri-Ranganadi area in the foot-hills of tho Assam Himalaya are briefly mentioned. The age of the Gondwana sediments of the Himalayan rogion in the north-eastern parts of India and the probable palaeogeographical conditions that prevailed at tho time are also discussed.

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THE STRUCTURAL AND DRAINAGE PATTERNS OF THE WESTERN GHATS IN THE VICINITY OF THE PALGHAT GAP

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THE STRUCTURAL AND DRAINAGE PATTERNS OF THE WESTERN GHATS IN THE VICINITY OF THE PALGHAT GAP[1]

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Contents

I. Introduction

The Palghat Gap which lies across the Western Ghats in Malabar, forming the only major break in the continuity of the high hills and connecting the West Coast with the rest of the Madras State, is a noteworthy feature in the physiography of southern India. The nature and the mode of origin of the gap is an interesting problem in the geology of southern India which has hardly received any serious attention. No detailed geological mapping of the area of the gap and the adjoining high hills has been carried out till now.

A study of the one-inch and quarter-inch topographic maps of the region has brought to light the remarkably interesting drainage pattern in the hills immediately to the south of the Palghat Gap. The alignment of certain streams and groups of streams with intervening cols along two or three lines forming straight linear patterns of some considerable extent, would seem to indicate possible lines of shearing or faulting. A careful study of the trend lines in relation to the physiography, drainage and geology of the area reveals many striking facts and has enabled us to arrive at certain tentative conclusions regarding the evolution of the drainage pattern of the area and also the possible origin and the age of the Palghat Gap.

II. Physiography of the Area

Physiographically the peninsular area south of Mangalore, with which we are concerned, may be divided into three broad natural divisions, (1) the narrow strip

[1] Published by permission of the Director, Geological Survey of India.
Dr. S. L. Hora, Director, Zoological Survey of India, after studying the fish fauna of the hill streams of the Western Ghats, has arrived at certain interesting conclusions regarding their distribution on either side of the Palghat Gap. On discussing with him the geological aspects implied in the distribution of the hill stream fauna, we were stimulated to search for evidence which may throw some light on the structure and the possible age of the Gap.

of coastal plains of South Kanara, Malabar, Cochin and Travancore, (2) the high ranges of the Western Ghats with a narrow gap at Palghat, and (3) the broad undulating plains of South Madras comprising the districts of Coimbatore, Salem, Madura, Trichinopoly, Ramnad and Tinnevelly.

(1) *Coastal Plains.*—The plains along the West Coast extend continuously from Bhatkal port north of Mangalore as far as Cape Comorin at the southern tip of the Peninsula. In the Mangalore region, the coastal plain is 5–8 miles in width, but it narrows down to a strip of only 2 miles near Kasargod. South of Cannanore the plain broadens out and in the region between Calicut and Quilon, reaches a width of nearly 15–20 miles. Between Trivandrum and Nagercoil in the south, it again narrows down to 6 or 8 miles. A section across the coastal plain from east to west reveals four sub-divisions, (*a*) a steeply sloping, partially forested country formed of hills and ridges immediately at the foot of the ghats, followed by, (*b*) an undulating tract with water-logged paddy fields interspersed with low hillocks and mounds of laterite, succeeded by, (*c*) a flat raised tract (3–6 miles) capped with laterite and underlain by sub-recent sediments towards the coast, (*d*) the regions between Ponnani and Cochin, and between the latter and Quilon are marked by the backwaters parallel to the coast.

(2) *Western Ghats.*—The Western Ghats extend as a range of high hills, 15–30 miles in width, over a distance of nearly 450 miles in a NNW-SSE direction from near Karwar on the Bombay border to Cape Comorin in the south. The highest peaks are the following:—

South Kanara: Kodachadri (4,402) and Kuduremukha (6,207).
Coorg: Pushpagiri (5,620).
Nilgiri: Vavulmala (7,673), Doddabetta (8,640), Kolarbetta (5,624).
Nilgiri-Malabar border: Gulkal (8,090), Anginda (7,817), etc.
Cochin: Karimalai Gopuram (4,721).
Anaimalai hills: Anaimudi (8,841), Tanakamalai (8,244), etc.
Kodaikanal hills: Ibex Peak (8,663), Vembadi Shola Peak (8,221), Kodaikanal Peak (7,664).
Andippatti-Varshanad hills: Surulimalai (5,680), Suruliparai (6,221).
North Travancore-Tinnevelly border: Kottaimalai (6,624), Sivagirimalai (5,723) and Devarmalai (6,307).
South Travancore-Tinnevelly border: Vairattimotti (5,237), Agastiyamalai (6,132) and Mahendragiri (5,427).

The general trend of the ghats is NNW-SSE and there are three more or less arcuate projections extending eastward into the South Madras plains: (*a*) the Nilgiri range running ENE between the Coimbatore plains and the Mysore plateau, and continued northward into the Satyamangalam-Kollegal hills of Madras and Biligirirangan Hills of Mysore, (*b*) the Palni range (Kodaikanal hills) running also ENE and continued east and ESE, after a narrow pass at Dindigul, into the Sirumalai-Ammayanayakkanur-Ayyalur hills, and (*c*) the low Varshanad-Andippatti range running NE towards the Vaigai valley. Lying between the arcuate projections of the Nilgiri range and the Anaimalai-Palni range is the Palghat Gap, with an elevation of 250–1,000 ft., the highest point in the gap being a little over 1,000 ft. near Pollachi.

(3) *Plains of South Madras.*—The plains to the east of the ghats comprising the districts of Coimbatore, Salem, Trichinopoly, Madura, Ramnad and Tinnevelly, form a broad undulating region sloping gently to the east and south-east towards the Bay of Bengal and the Gulf of Manaar. These fall into two divisions, (*a*) the Coimbatore-Salem-Trichinopoly region lying between the Nilgiri-Satyamangalam hills in the north and the Palni hills to the south, and (*b*) the Madura-Ramnad-Tinnevelly region to the south, separated from the northern region by the projection of the Palni-Varshanad-Andippatti ranges. Between the Palni and the Andippatti

hills lies the narrow Kambam valley. The general elevation of the northern plain is between 500 and 1,000 ft., while that of the southern is between 250 and 500 ft.

III. Climate

The area has an equable temperature ranging between 75° and 100°, the mean for the year being 80°–90°. February to May is the hot season when the temperature rises to 90°–100°; between December and January is the cold season with a temperature range of 70°–77°. With regard to rainfall, there is great contrast between the West Coast and the plains to the east of the ghats. The south-west monsoon breaks on the West Coast at the end of May and for three or four months the region is in the full grip of the monsoon. The annual rainfall, which is mostly received during this period, goes up to 200 inches. The South Madras plains, being on the leeward side of the ghats, receive practically no rainfall during the south-west monsoon except around the Palghat Gap and the high passes as in the Kambam valley and around Shencottah. Only strong dry westerly winds prevail here during this period which lower the summer temperature considerably. The rainfall on this side is around 35 inches, the greater portion of which is received during the north-east monsoon in October, November and December. During this period, the coastal region immediately adjoining the Palghat Gap is subjected to dry easterly winds and dust storms.

IV. General Drainage

The drainage of the region is in conformity with the three physiographic divisions, with the summit of the Western Ghats forming the natural divide between the drainage systems of the West Coast plains and the South Madras plains.

The rivers and streams along the western slope of the ghats flow west and north-west and, on emerging into the coastal plains, run west or south-west into the Arabian Sea within a short distance from their source in the hills. The most important of these rivers are the Netravati and Payaswani in South Kanara, the Valarpattanam, Beypore and Ponnani (Bharata Puzha) in Malabar, the Chalakkudi Ar and Periyar in the Cochin region, and the Manimalai Ar (Pamba Ar), Achankovil Ar and Kodayar in Travancore. Owing to the heavy rainfall along the western slopes of the ghats, the rivers and streams on the West Coast are perennial. Their course from the hill slopes to the sea is short and steep, and they flow rapidly into the sea cutting steep valleys.

The rivers and streams of the South Madras plains have their sources on the steep eastern slopes of the ghats and they flow east or south-east towards the Bay of Bengal, Palk Strait or the Gulf of Manaar. They flow with only moderate currents and have developed long broad valleys. Having their source on the leeward side of the ghats which receives only a low rainfall, the majority of the rivers and streams, except the Cauvery, are dry during the greater part of the year and are flooded only during the monsoon.

In relation to the two sub-divisions of the region, the drainage systems are also quite separable. The chief rivers of northern region are the Bhavani from the Nilgiri hills, the Noyyal from the Coimbatore hills and the Amravati from the Anaimalai hills. These flow east or north-east into the Cauvery which enters this region from the Mysore plateau after cutting through the Kollegal hills and flows south, south-east and east between the districts of Salem, Coimbatore and Trichinopoly.

The important rivers of the southern region are the Vaigai from the Cardamom hills, the Vaippar from the Sivagiri hills, the Chittar from the Tenkasi hills and the Tambraparni from the Papanasam hills. All of them flow south-east into the Gulf of Manaar. The Vaigai is the longest river in the area. Rising from the Periyar

lake on the eastern slopes of the Cardamom hills, as the Suruli Ar, it flows north-east through the Kambam valley for nearly 50 miles and then turns south-east as the Vaigai river flowing through Madura and entering the sea not far from Ramnad town. The details of drainage of the area adjoining the Palghat Gap are given in Sections VII and IX below.

V. Geological Formations

The geological formations of the area belong to the Pre-Cambrian metamorphic complex with a narrow belt of sedimentaries along the coastal region. The Pre-Cambrian rocks consist of granitoid mica-gneisses and garnetiferous gneisses, with broad massive bands of charnockitic rocks, and thin bands and lenses of hornblende and biotite schists, granular quartzites, crystalline limestones and calc-granulites, and metamorphosed rocks of igneous or sedimentary origin including pyroxene granulites, epidiorites, etc. The northern part of the region, comprising the districts of South Kanara, Malabar, Cochin, Nilgiris, Coimbatore, Salem, Trichinopoly and Madura, shows a more predominant development of granitoid biotite-gneisses, while the area to the south is chiefly composed of garnetiferous gneisses. A few lenses and masses of ultrabasic rocks like pyroxenites, amphibolites and dunites are also found. Pink granites and granitic gneisses of a late age (equivalent to the Closepet granites of Mysore) occur amidst the gneisses of both the regions, but more commonly in the north. With these granites are associated some younger pegmatites and quartz veins which carry at places mica, gemstones and rare-earth minerals like allanite and columbite-tantalite.

The sedimentary formations along the West Coast are of small thickness and of Recent and sub-Recent age, except for the Miocene Warkalai and Quilon beds. The lignites of Beypore and Cannanore are probably also of the same age.

The rocks of the South Madras plains are not weathered to any considerable extent and the country commonly displays good outcrops. The soil and alluvial mantle, except along the river valleys, is very thin, ranging up to 10 feet in thickness. The summits of the Western Ghats and the steep eastern slopes of the range are also composed of barren precipitous rocks with only a thin capping of soil.

Conditions are different on the West Coast and on the western slopes of the ghats, owing to the heavy rainfall and thick vegetation. The soil cover in the West Coast plains is on an average 50 ft. in thickness and there is also a thick capping of laterite in many places, especially on the western slopes of the ghats, the higher regions of the ghats being composed of barren unweathered rocks.

VI. Geological Structure

(Text-figs. 1 and 2)

The trend lines of the rocks together with the broad physiographic features and geology are shown in the accompanying sketch map (Text-fig. 1).

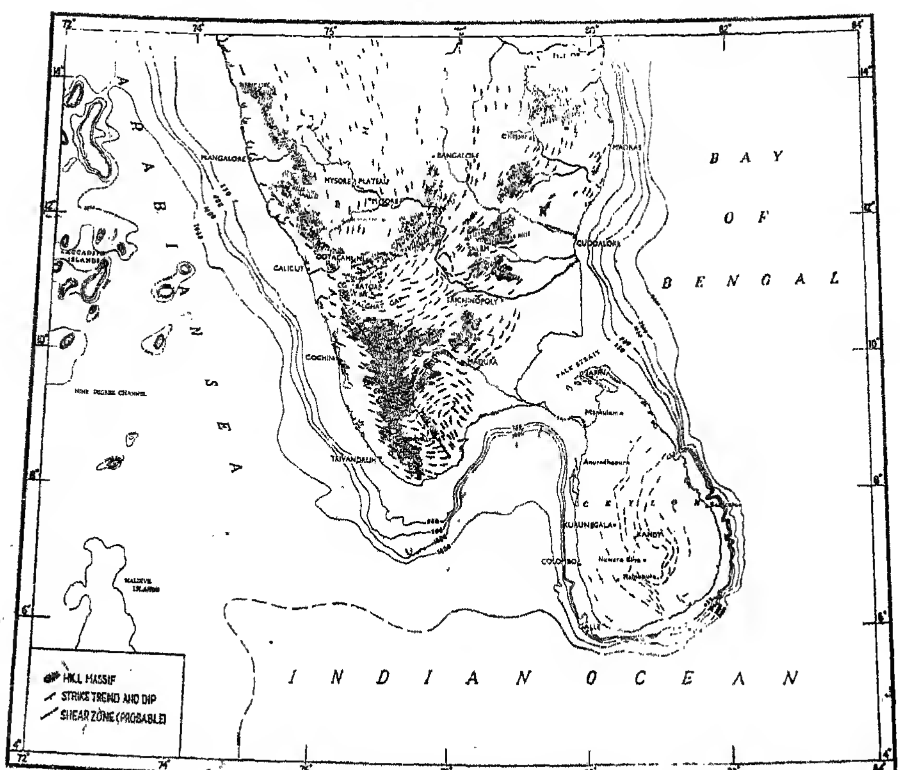
The strike of the rocks in the coastal plains and along the western slopes of the ghats is generally NW-SE, varying between NNW-SSE in North Kanara and Coorg, NW-SE in Malabar and North Travancore, and WNW-ESE in the South Travancore region. About a NNW-SSE imaginary line passing through the summit of the Western Ghats, through Coorg, Wynaad, Anaimalai hills, Periyar lake and Tenkasi town, there is a sudden change in the trend of the rocks due to folding about a north-south axis. From a NNW-SSE or NW-SE trend on the western side of the ghats, the strike veers round to the east, ENE and finally to NE on the eastern side. The strike of the North Malabar-Coorg rocks continues into the Nilgiri range in a ENE direction. This is continued further on into the NNE (and occasional

northerly strikes) of the Satyamangalam-Biligirirangan-Kollegal hills along the Mysore border. The rocks of the Palghat Gap region continue similarly into the Coimbatore plains and turn gradually with a NE strike into the Salem region. This north-easterly trend extends from the Shevaroy-Kalrayan hill tracts of Salem into the Javadi-Yelagiri hills of South Arcot and is continued into the neighbourhood of Chingleput and Madras city. Similarly the NW-SE strike of the South Malabar-Cochin rocks continues east and ENE into the Anaimalai and Palni hills and further up into the Trichinopoly-North Madura region in a NE directions, beyond which it is concealed by younger rocks. The NW-SE strike of the North Travancore rocks turns round to the NE into the Kambam valley, Andippatti-Varshanad hills and West Ramnad plains beyond which the Archaeans are covered by Tertiary sediments. The NW-SE and WNW-ESE trends of South Travancore extend into the South Tinnevelly plains and gradually curve round to an easterly direction towards the coast where they become concealed underneath the sub-recent coastal deposits.

The general regional trend of the rocks in South Madras plains some distance east of the Western Ghats is thus NE-SW. But about a roughly north-south irregular line passing through Erode, Dindigal, Madura city, Virudhunagar and Kovilpatti, there is a northerly loop in the strike of the rocks due to folding of the strata about a north-south axis, similar to the one noticed along the Western Ghats (Text-fig. 1).

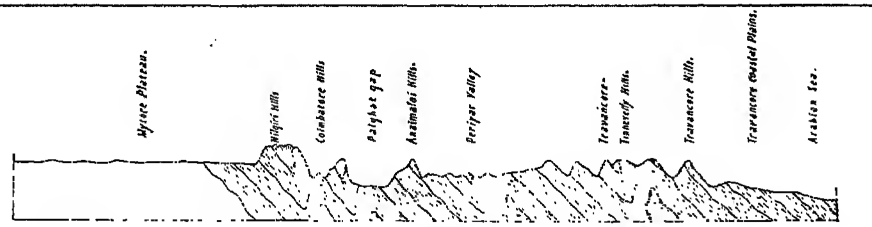
TEXT FIG.1—PROVISIONAL TECTONIC MAP (PRE-CAMBRIAN) OF PARTS OF PENINSULAR INDIA AND CEYLON

SCALE 1"=100 0 20 40 60 80 100 120 140 MILES



The general regional dip of the rocks is to the WSW, SW and SSW in the West Coast region, which changes to south, SSE and SE in the South Madras plains. Opposing northerly dips, i.e., to the NW, NNW, north, NE and ENE, are often found along certain areas as a result of local folding. Along the north-south fold axis in the region of Erode-Madura-Kovilpatti, the dips are rather confusing due to the variations in the nature of the folding at different places. The dip is generally steep to moderate. In the West Coast region, it varies from 80°–60° in South Kanara, Coorg and Malabar to 60°–50° in Travancore. In the South Madras plains the dip ranges from nearly vertical to about 50°–60°, and as in the West Coast region, there appears to be slight flattening of the dips as we proceed southward.

The rocks of the Mysore Plateau on the northern side of this region strike NNW-SSE. The Dharwarian schists form linear belts amidst the gneissic and granitic rocks as north-pitching synclinal folds with the intervening anticlinals eroded away. Structurally this region appears to represent the eroded portion of a main anticlinorium.



A GENERALISED SECTION ALONG THE WESTERN GHATS SHOWING THE GEOLOGICAL STRUCTURE (HYPOTHETICAL)

SCALE 32 16 0 32 64 96 MILES

Text Fig. – 2

A careful study of the map seems to indicate that the strike trends of the rocks of South Madras closely follow those of the Dharwar schist belts. The schistose formations thus seem to form the basal portion of the Dharwar schists which may probably rest on older formations. The general structure of the region is that of a series of major anticlines and synclines with minor folds on the limbs of the major ones. In conformity with the Dharwar synclines, these folds should also plunge to the north. The southerly loop in the strike of the rocks about the Western Ghats and in the vicinity of the Palghat Gap thus appears to be a north pitching synclinal fold and the northerly loop about Erode, Madura and Kovilpatti is a north-pitching anticlinal.

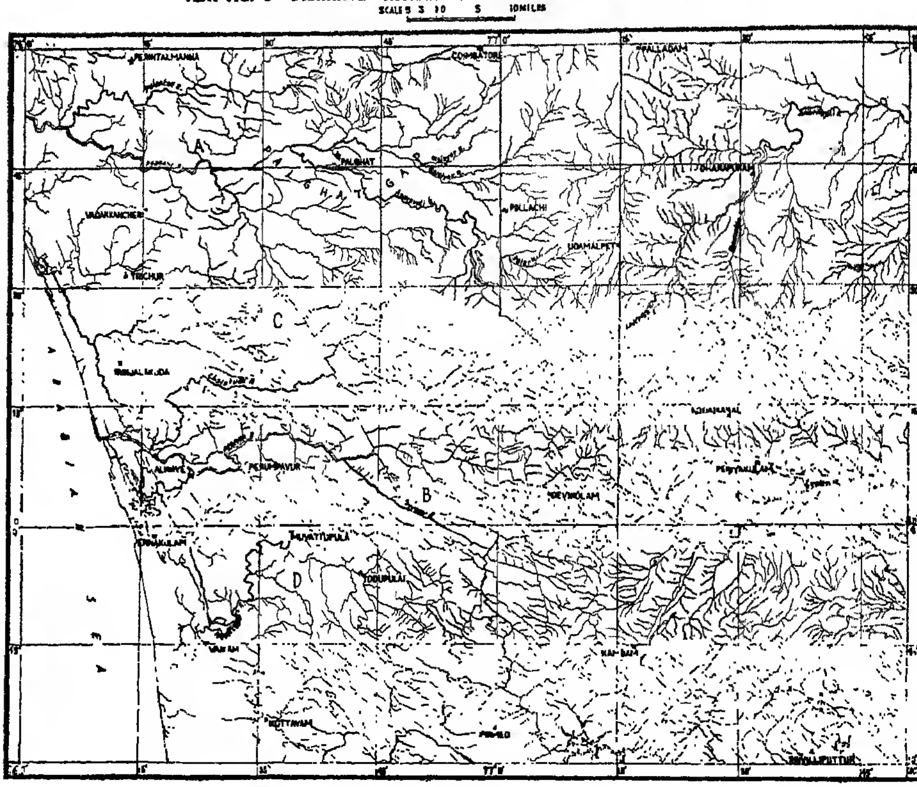
VII. Drainage pattern in the Hill Tracts adjoining the Palghat Gap and its possible explanation

(Text-figs. 3–6)

A study of the topographic maps of the West Coast and the western slopes of the ghats of this region reveals that the majority of the rivers and the larger streams flow in a general westerly and north-westerly direction in their course through the hills following the strike of the rocks. In the coastal plains which are covered with a thick mantle of alluvium and laterite and sub-Recent formations, the streams have a low gradient towards the sea, preferring no particular directions.

In contrast with the general direction of flow of these main streams, are other smaller streams and tributaries which join the main drainage at high angles cutting across the general trend of the hills and the direction of strike of the rocks. The hill tracts of South Malabar and Cochin lying immediately to the south of the Palghat Gap are of interest in this respect, (Text-fig. 3).

TEXT FIG. 3—DRAINAGE PATTERN OF THE AREA AROUND PALGHAT GAP.



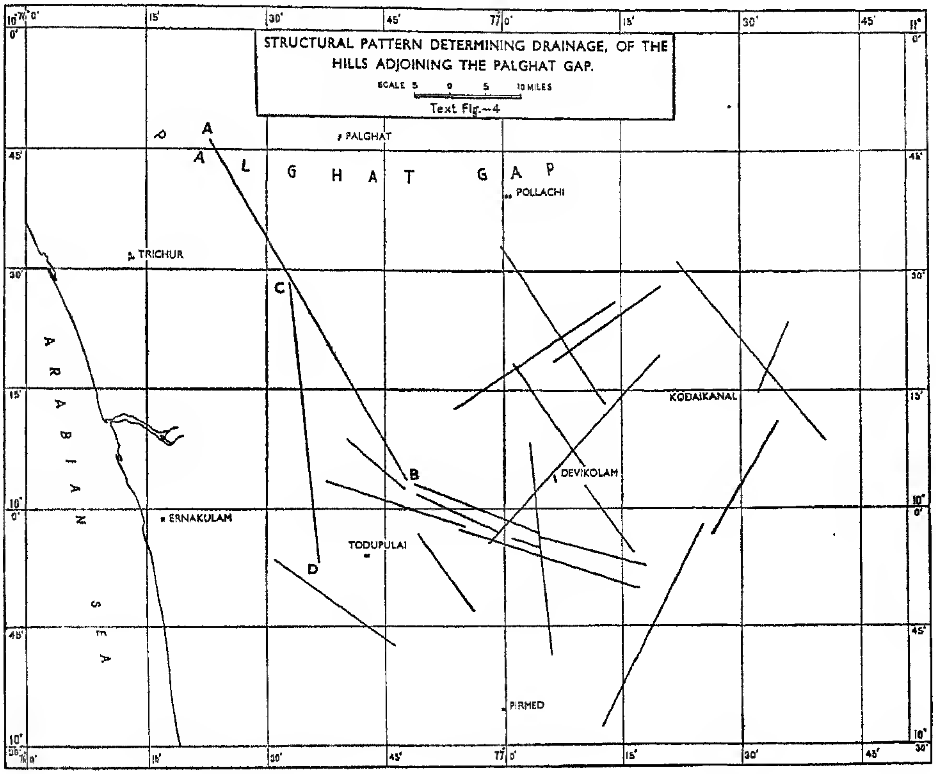
The main streams in this region running west and north-west are (1) the Bharata Puzha in the Palghat Gap, (2) the Mappili Puzha and Parambikolam Ar (along the sides of which the government timber tram line runs), (3) the Chalakudi Ar, (4) the Yedamalai Ar, (5) the Puyankutti Ar and (6) the Periyar.

Meeting these rivers at fairly wide angles are two sets of prominent tributaries, (1) the Gavitri Puzha, the Karappara Ar, the connecting streams between Parambikolam Ar and the Chalakkudi Ar and between the northern and southern sections of the Yedamalai Ar and a few others extending in a NW-SE line between the Bharata Puzha and the Periyar; (2) the Kannankuzhi Todu, Perum Todu, Kottapara Todu and a few others running in a N-S line. The courses of the main streams are also marked occasionally by sharp bends which offset the streams for short distances. Groups of waterfalls and cascades are found not only along the main streams but also in the tributaries, particularly near their junctions.

The remarkably straight alignment of the tributary streams (A-B, C-D: in Text-figs. 3, 4) mentioned above is very striking. These are streams (with intervening cols) which take part in the linear patterns. One set lies in a NW-SE direction extending for nearly 64 miles (A-B, Text-figs. 3, 4) and the other in a N-S direction running for a distance of 32 miles (C-D, Text-figs. 3, 4). The two sets converge at the western end of the Palghat Gap area. They probably represent certain well defined structural features.

The northern ends of both may be traced to the actual gap where the height above mean sea-level is only 500 ft. As the straight river patterns are developed between altitudes of 500 ft. and 5,000 ft. above sea-level, it is not improbable, as

Auden (1951, p. 35) pointed out, that the structural features are of great lateral extent, and are developed through a considerable vertical range. In the case of a NE-SW linear pattern extending for nearly 40 miles and which passes near Mattupatti dam site in Travancore, Auden estimates a vertical range of 6,200 ft.



STRUCTURAL PATTERN DETERMINING DRAINAGE, OF THE HILLS ADJOINING THE PALGHAT GAP.

Text Fig.—4

Similar straight alignments, but less striking, are also noticed in the upper reaches of the Yedamalai Ar and Puyankutti Ar, and also at places in the Anaimalai-Devikolam hills. As seen in Text-figure 4, four major directions may be recognized in the linear stream patterns developed in the region to the south of the Gap.

The first impression conveyed by these linear patterns is that they are possibly fault planes. A careful examination of the valleys along the Mappili Puzha and Parambikolam Ar during a traverse along the timber tram line has, however, not indicated the presence of such later faulting. The rocks here are foliated and banded gneisses with charnockitic bands, and have a general WNW-ESE, E-W and ENE-WSW trend with low dips of about 20°–30° generally to the south. The gneissic and charnockitic bands are clearly seen traversing the beds of these tributaries without any lateral shifting or other signs of disturbance. No indication of any fault could be noticed in the vicinity of Ottappalam along the Bharata Puzha west of Palghat where the NW-SE line appears to terminate.

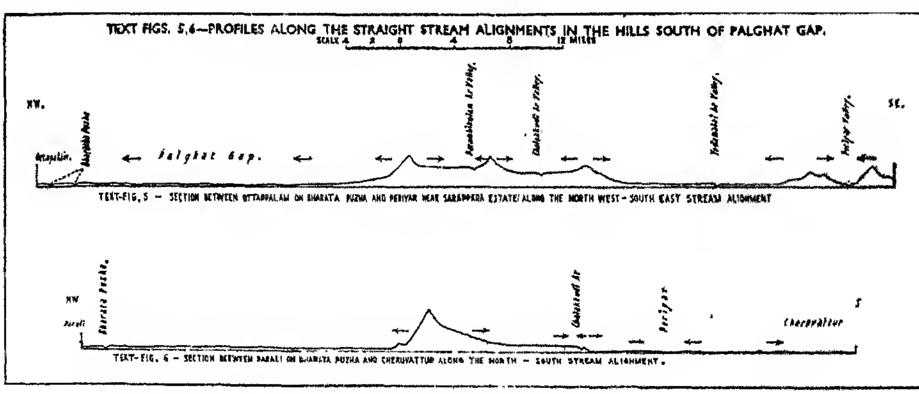
Auden (51) had, however, observed a shear zone about 70 ft. in width near the Mattuppatti dam site through which a NE-SW linear pattern runs. He could not find any convincing evidence of major fault offsets having taken place along this zone.

A careful study of the map reveals that the linear patterns (A-B, CD, in Text-figs. 3, 4) are more or less at right angles to the strike directions of the rocks and they occur in greater numbers at the north-pitching synclinal fold, where the strike of the rocks changes from NW-SE and WNW-ESE to E-W and ENE-WSW. It is possible, therefore, that the linear patterns may be the result of shearing.

Shearing may occur more or less uniformly along a straight boundary for considerable length. It may also follow the easiest planes of weakness in the rocks which, in this case, are at right angles to the strike. Such shear fractures most probably determined the straight courses of the tributaries in contract with the courses of the main streams which follow the strike of the rocks. Elsewhere, these fractures might have encouraged block-faulting, so that one may reasonably expect to find them indicated by long straight segments of streams begun or ended by abrupt bends. If one examines carefully the other parts of the Western Ghats, more examples may come to light. In this connection the recent papers by Radhakrishna (1952) and Radhakrishna and Ghouse (1951) may be seen. An extended study of the stream patterns, particularly of the region south of the gap, should be worthwhile.

It may be pointed out here that during the course of systematic mapping in the Tinnevelly district, a 'thrust' zone of presumably Pre-Cambrian age has been recognized by one of us (S.N.) running in a NW-SE direction for a distance of over 120 miles (Text-fig. 1). This zone is traced from the Tambraparni river near Srivaikuntam up to the foot of the Western Ghats north of Srivilliputhur. Except for a slight lateral shift in its alignment in the hills near the Periyar lake region, the 'thrust' zone recognized here apparently extends in continuation of the major shear line (Text-fig. 4, A-B; Text-fig. 1) noticed in the Palghat Gap region.

To our mind an alternative explanation of the linear stream patterns immediately to the south of the Gap is to consider them as remnants of an original drainage much older than the main streams. The present west and north-west flowing streams like the Periyar, Chalakkudi Ar, Bharata Puzha, etc. are apparently subsequent to the faulting of the West Coast region and these have followed the strike directions of the rocks. The direction of flow of the tributaries which make the straight line patterns appears to have no definite relation to the main streams which they join. The sections shown in Text-figs. 5, 6 are drawn along the lines of tributaries extending south-east



TEXT FIGS. 5,6—PROFILES ALONG THE STRAIGHT STREAM ALIGNMENTS IN THE HILLS SOUTH OF PALGHAT GAP.

TEXT-FIG. 5 — SECTION BETWEEN OTTAPPALAM ON BHARATA PUZHA AND PERIYAR NEAR SARAPPKRA ESTATE ALONG THE NORTH WEST – SOUTH EAST STREAM ALIGNMENT

TEXT-FIG. 6 — SECTION BETWEEN PARALI ON BHARATA PUZHA AND CHERUVATTUR ALONG THE NORTH – SOUTH STREAM ALIGNMENT.

and south from the Bharata Puzha to the Periyar. A study of these profiles shows that the divides between the opposing pairs of tributaries gradually decrease in elevation as one proceeds southward, and the south-flowing tributaries are much longer than the north-flowing ones. These features perhaps indicate the possible existence in the past of south-east and south flowing main streams which occupied

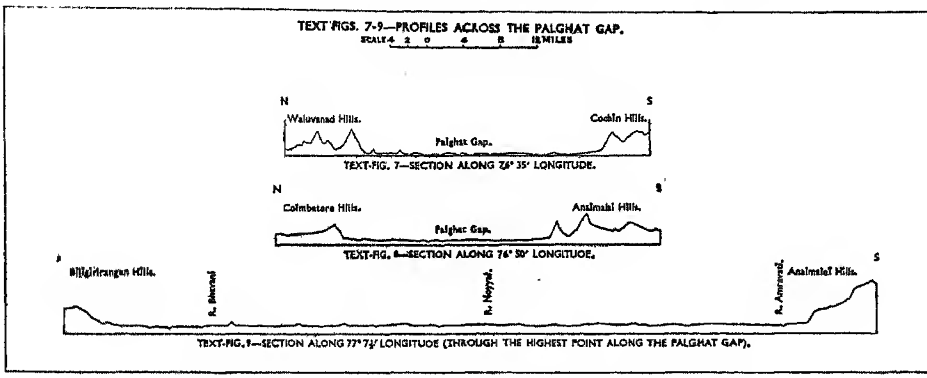
these valleys at a much higher elevation than at present. They were consequent upon the original slope of the terrain. Subsequent to the faulting and tilting of the West Coast region, these streams might have considerably dwindled in size, probably because the sea encroached upon the area to the west stimulating the development of west-flowing streams. They now occupy the position of the old valleys as tributaries meeting the west and north-west flowing main streams formed at a later period.

A recent paper by West (1951) has come to our notice wherein the author mentions having recognized paired shear fractures *en echelon* over a wide area in Alaska, which at times determine straight stream directions. The author has also attempted to determine the direction of inferred force. In the case of the shear fractures recognized in parts of South India we are at present not in a position to determine the direction of force without additional data.

VIII. The Evolution of the Palghat Gap

(Text-figs. 1, 4, 7–9)

As mentioned in an earlier section, the Palghat Gap is a fairly undulating pass extending east to west with an average width of eight miles (Text-figs. 1, 7–9). The elevation of the gap ranges from 250 ft. near Palghat to a little over 1,000 ft. at Pollachi (Text-figs. 7–9). The hills on either side rise abruptly as steep precipitous scarps reaching to heights of over 3,000 ft. The almost straight direction of the



TEXT-FIGS. 7-9—PROFILES ACROSS THE PALGHAT GAP.

TEXT-FIG. 7—SECTION ALONG 76° 35′ LONGITUDE.

TEXT-FIG. 8—SECTION ALONG 76° 50′ LONGITUDE.

TEXT-FIG. 9—SECTION ALONG 77° 7½′ LONGITUDE (THROUGH THE HIGHEST POINT ALONG THE PALGHAT GAP).

hills and their steepness on either side of the gap, especially to the south, might suggest that faulting in an E-W or NE-SW line was responsible for the formation of the gap. A study of the strike trends and other features apparently does not support such a suggestion for the origin of the Palghat Gap. No trace of faulting has been noticed in the rocks of the Coimbatore region immediately to the east of the gap. From a NW-SE trend on the West Coast the rocks turn eastwards through the gap and run east and ENE into the Coimbatore region. It appears, therefore, that evidence for the evolution of the gap has to be searched for in the physiography and the drainage features of the area.

The river Cauvery which forms the main drainage basin here, flows to the south-east and east through the Coimbatore-Trichinopoly plains, between the Nilgiri-Satyamangalam-Salem hill tracts in the north and the Palni-Dindigal hills to the south. The rivers Bhavani, Noyyal and Amravati are the main tributaries which enter the Cauvery from the western side after draining the Coimbatore plains. The combined basin of these tributaries is a broad undulating peneplain.

The major portion of the area receives a low rainfall and the rivers are flooded only for a short period during the rainy season. It is really difficult to conceive of such a broad peneplain developed by denudation by these rivers alone. The shape and size of the basin and its general slope towards the east seem to suggest that it was once occupied by a larger stream flowing eastwards right from the Palghat Gap and receiving a much greater flow of water from the hills to the west.

A study of the contours also indicates that this stream probably occupied the course of the present Amravati river between Karur and Dharapuram, and the Uppar Odai between Dharapuram and Pollachi. The course of the stream further west was probably through the centre of the Palghat Gap with a gradual northerly turn towards its source just above the region of Anangamalai (△ 1291). The Bhavani and the Noyyal were probably its tributaries which entered the main river from the north.

After the faulting and the subsequent tilting of the West Coast region resulting in the diminution of the water supply from the hills to the west, this Ur-Cauvery might have become considerably dried up. Depending on the degree and direction of tilting, the ancient Cauvery appears to have captured the present stream from the Mysore plateau after cutting its way through the Kollegal-Biligirirangan hills.

The existence of deep gorges like the Mekedatu and waterfalls like Sivasamudram and Hoganakal seems to point to the still youthful stage of the Cauvery in this region. The alternate straight courses of the river following the strike of the rocks, followed by sharp bends cutting across the strikes with deep gorges and waterfalls, apparently indicate a subsequent drainage.

The original east flowing river might have gradually dwindled in size leaving only a steep-sided wind gap in the Palghat region. The profile section across the gap (Text-figs. 7–9) reveals steep and almost precipitous slopes on either side down to 1,000 ft., below which occurs the almost flat valley of the Bharata Puzha.

In addition to the easterly drainage, the probable presence of a large westerly flowing drainage system with its source very close to the Palghat region is indicated by the landward curvature of the bathymetric contours in the region of the Arabian Sea opposite to the gap and continued WSW to a deep channel, 'the Nine Degree Channel', between the Laccadive and the Maldive groups of islands (Text-fig. 1). The significance of this submarine depression which may possibly indicate a submerged river valley is discussed in Section IX below. Medlicott and Blanford (1893, p. 495) had postulated the possible existence of a large westerly flowing river running through the Palghat Gap area, its main drainage having been reversed by earth movements which 'raised' the Western Ghats. They suggested that probably these movements considerably reduced the former westerly flowing river into the much smaller stream, the present Bharata Puzha, while the major part of the drainage was diverted to the east.

In explaining the accumulation of the ancient alluvium in the plains of the Narbada, of Berar and of the upper Godavari, Vredenburg (1906, pp. 38, 39), on the other hand, postulates the formation of a shallow anticlinal ridge running west of the western termination of the Narbada and Purna plains with a strike slightly east of north, instead of a general tilting of the western side of the Peninsula. Warping, as suggested here by Vredenburg, cannot explain many other remarkable features on the West Coast. No doubt there are evidences of warping in the western half of the Peninsula, but we feel that tilting has also taken place to some extent. In our opinion tilting and warping of the western parts of the Peninsula followed the block faulting.

The drainage systems mentioned above followed the general slope of the land, and their direction had, therefore, been to the east, south and west. Subsequent to the faulting on the West Coast, a new set of west-flowing streams developed from the steep western slopes of the ghats. These streams followed the weak planes of the rocks which now naturally lie along the strike, viz., to the west and NW.

The Bharata Puzha is one such subsequent stream which has developed along the old gap in the Palghat region. It is now cutting headward into the gap and on to the Coimbatore plains, and its tributaries have their origin from the slopes of the Anaimalai hills south of Pollachi. As may be seen from the section in Text-fig. 9, the only remnants of the original east-sloping valley floor which have withstood erosion and occur as isolated stumps are: (1) the 1,250 ft. high-ground ENE of Pollachi, and probably (2) the ridge Anangamalai (1,500 ft.) to the NE of Shoranur.

In a recent contribution by King (1950, pp. 109–111) on the study of the world's plainlands, the author suggests the existence of three cyclic erosion surfaces in the Indian Peninsular region. In southern India he recognizes a 'Gondwana Cycle' of levelled residuals of Gondwana age in parts of the Nilgiri and Cardamom hills, rising above the general plateau ('Indian Cycle') which he considers to be younger. According to him, the 'Gondwana' land surface is pre-Cretaceous while the 'Indian' land surface is Cretaceous-Middle Tertiary. The Palghat Gap area is shown in his map as 'post-Indian' land surface of late Tertiary-Recent age. In our opinion, King's views require scrutiny before they can be accepted. However, it is of interest to note that the N-S and NW-SE linear drainage patterns observed in the Palghat Gap area cut across the 'Indian' (Cretaceous-Middle Tertiary) and 'post-Indian' (late Tertiary-Recent) land surfaces. To those who find King's views acceptable, it may appear that any shearing that might have been responsible for these linear patterns, probably took place not earlier than the late Tertiary. On the other hand, it is not unlikely that a more ancient feature of the land was rejuvenated in comparatively recent time.

IX. Bathymetric contours in the Arabian Sea west of the Palghat Gap

(Text-fig 1)

It is noteworthy that in the region due west of the Palghat Gap in the Arabian Sea, the 200, 500, 1,000 and 5,000 ft. bathymetric contours take a more or less sharp bend towards the coast, thereby suggesting that in this region a submarine valley exists (Text-fig. 1). Further west, between the Laccadives and the Maldives this valley probably extends in a WSW direction as the 'Nine-Degree Channel'. The alignment of this channel and the prominent deflection of the bathymetric contours towards the region of the coast west of the gap, is approximately in the ENE-WSW direction.

This interesting feature may at first suggest the existence of a submerged valley formed by a large river which once took its course through the gap (as postulated in an earlier chapter) in a WSW direction and extending into the region of the Arabian Sea.

It would appear that the Pleistocene changes of sea-level owing to the repeated formation on land of thick ice sheets and their melting, would only account for an oscillation of sea-level of about 300 ft. It is possible that during the low sea-levels of the Pleistocene Ice Age the upper parts of the submarine valley were incised when the shelf surface was largely situated at or above sea-level.

According to Bourcart (1938), continental flexure has apparently taken place along their margins causing periodical marginal flexure or bowing upwards of the borders of the continents, accompanied by submergence of the margins resulting in rejuvenation of the continental border relief. Jessen (1934) has also supported this idea. Such rejuvenation has been a characteristic feature of comparatively recent geological times. But these movements caused by subsidence of the shelf areas and the uplift of the coastal regions can only be small in amplitude.

On the other hand, if we assume a N-S coastal block faulting with crustal subsidence from a normal level, we shall have to postulate a downthrow of at least

5,000 ft. magnitude to account for an erosion base at that depth. It may be that the theories based on sub-aerial origin alone, explaining the present level of the submarine valley, will have to be abandoned.

In a subsequent section, we have attempted to adduce evidence for the Lower Miocene faulting of the West Coast, although some hold the view that this event took place in the Pliocene or Pleistocene times which may be true of only the Mekran Coast.

Though the faulting is of Miocene age, it would seem that the submerged land had preserved some of its erosional features such as the postulated ENE-WSW drowned river valley extending from the Palghat Gap area towards the 'Nine-Degree Channel'. In the present state of our knowledge, it is difficult to decide whether to consider this feature as a mere submerged river valley or as something else. However, as Kuenen (1950) has pointed out, 'Conditions under water may possibly tend to encourage the development of forms that are destroyed on land. The absence of weathering and to a large degree of the creep of surface layers on the sea floor should allow bold forms to persist almost indefinitely that would soon crumble away under the influence of atmospheric attack'. It is therefore quite possible that gullies and valleys of a former land surface may persist under submarine conditions for a much longer period than similar features on the land. Hence the submarine surface features now seen may reflect those present on the land surface in the Miocene just before the land was faulted down.

The Laccadives and the Maldives which for the most part arise from two separate plateaus (Sewell, 1935, p. 42) with the former at a depth of about 1,000 fathoms and the latter about 1,900 fathoms (Gardiner, 1902, p. 296), are not exactly in the same alignment; the latter group of islands lie slightly displaced to the east from a perfect N-S alignment. The 'Nine-Degree Channel' between the two groups of islands may possibly represent a drowned valley occupying a zone of an ancient fault line, the displacement extending ENE opposite to the Palghat Gap area. It has also been suggested by Davis (1928, p. 525) that the Laccadive and the Maldive atolls and reefs are perched on the tops of fault blocks (Sewell, 1935, p. 435).

In our opinion, major changes in sea-levels on the West Coast were caused by several factors including subsidence of land after the block faulting, eustatic changes during the Pleistocene as a result of the formation and melting of large sheets of land ice mostly in the northern continents, and possibly also continental flexure.

X. Period of formation of the present West Coast and the probable age of the Palghat Gap

Subsequent to the faulting along the West Coast of the Peninsula, subsidence took place accompanied by brief incursions of the sea into the land. At that time the present West Coast region was worn back and a wave-cut platform resulted with the formation of wave-built terrace in front. If this surmise is correct the present plains lying immediately at the foot of the ghats represent the wave-cut platform and the laterite uplands towards the coast underlain by the marine sediments, the wave-built terrace. As the trend lines of the rocks are nearly transverse to the coast, drowning and marine denudation have resulted in long promontories alternating with narrow estuaries. This may be seen from the projecting ridges of harder rocks alternating with low narrow valleys at the foot of the ghats. As already pointed out by Medlicott and Blanford (1893, p. 11), the sea probably extended as a bay into the Palghat Gap thus augmenting the steepening of the walls of the gap.

These events were followed by the emergence of the West Coast which then began to expose the sediments deposited in the previous period.

From fossil evidence, the age of the Quilon beds on the West Coast is believed to be Burdigalian (Lower Miocene; Jacob and Sastri, 1951; Eames, 1950). The

characteristic Lower Miocene foraminifer, *Austrotrillina howchini* recently found in the Quilon beds (Jacob and Sastri, 1951) also occur in the Miocene of Broach on the Bombay coast (Rao, 1941). It is believed that the two patches are most probably of the same age (Lower Miocene). Near Ratnagiri also, between Quilon and Broach, marine Miocene sediments have been reported although their exact horizon is not definitely known. It would appear, therefore, that the faulting along the West Coast took place before the Burdigalian followed by marine incursion. The later emergence of the coast was in all probability post-Burdigalian.

Profiles drawn at intervals (1) from north to south across the Palghat Gap, and (2) from east to west along the West Coast plains from the sea to the Western Ghats seem to indicate some minor accordance of levels below 2,000 ft. altitude (Text-figs. 5, 6). These levels roughly correspond to elevations of 1,000 ft., 750 ft., 400 ft., and at intervals of 100 ft., between 400 ft. and the sea-level. The possibility cannot be overlooked that these levels may indicate different stages of emergence of the coast. The presence of groups of waterfalls along certain intermittent elevations inside the ghats also seems to have some relation with the suggested emergence in stages (Text-figs. 7–9). Further detailed study in the field will be necessary before any definite views may be expressed on the periods of emergence and other related phenomena.

In the preceding pages we have discussed at some length the possible significance of linear drainage patterns noticed in the Palghat Gap area, in the hope that it may focus attention on the desirability of taking up similar studies in other parts of India. Much of this paper is somewhat speculative. If, however, the views put forward, right or wrong, serve as a stimulus for further observations its purpose has been fulfilled.

Acknowledgement

We are grateful to Dr. M. S. Krishnan, Director, Geological Survey of India, for going through the paper and making valuable suggestions. We are also deeply indebted to Dr. J. B. Auden, Geological Survey of India, and to Mr. R. Tirunaranan, Madras Educational Service, for useful suggestions on various occasions.

Summary

The Palghat Gap which lies across the Western Ghats in Malabar, forming the only major break in the continuity of the high hills and connecting the West Coast with the rest of the Madras State, is a noteworthy feature in the physiography of southern India.

The physiography, general drainage, climate and the degree of weathering of the region are first described.

The geological formations of the area belong chiefly to the Pre-Cambrian metamorphic complex with a narrow belt of sedimentaries along the coastal region. The Pre-Cambrian rocks consist of granitoid mica-gneisses and garnetiferous gneisses traversed by broad massive bands and lenses of hornblende and biotite schists, granular quartzites, crystalline limestones and calc-granulites, all of which represent intensely folded granitized and metamorphozed remnants of original sediments and basic intrusive and effusive rocks.

The strike and dip of the rocks of south Madras closely follow the trend lines of the Dharwarian schist belts. The gneissic and charnockitic formations with the associated highly metamorphic rocks probably rest on older formation and have suffered the same degree of deformation as the latter. The general geological structure of the region is that of a series of major compressed anticlines and synclines, with minor folds on the limbs of the major ones. In conformity with the Dharwarian rocks, the synclinal folds in these rocks also plunge to the north. The southerly loop in the strike of the rocks about the Western Ghats in the vicinity of the Palghat Gap thus appears to be a north-pitching synclinal fold and the northerly loop about Erode, Madura and Kovilpatti is a north-pitching anticlinal.

In regard to the drainage pattern, the remarkably straight alignment of the tributary streams immediately to the south of the Palghat Gap area with associated waterfalls is very striking. One set of these lines lies in a NW-SE direction extending for nearly 64 miles and the other in a N-S direction running for a distance of 32 miles. They run more or less at right angles to the strike direction of the rocks at each place, and occur in greater numbers in the

north-pitching synclinal fold where the strike of the rocks changes from NW-SE and WNW-ESE to E-W and ENE-WSW direction. The two sets converge at the western end of the Palghat Gap area. It is surmised that there existed south-east and south flowing main streams which occupied these valleys at a much higher elevation than at present. They were probably consequent upon the original slope of the terrain. Subsequent to the faulting and tilting of the West Coast region, these streams might have considerably dwindled in size, probably because the sea encroached upon the area to the west. They now occupy the position of what are thought to be the old valleys of tributaries meeting the west and north-west flowing main streams formed at a later period.

It is suggested that the combined basin of the Bhavani, Noyyal and Amravati which join the Cauvery, is a broad undulating peneplain, once occupied by a larger stream flowing eastwards from the Palghat Gap and receiving a much greater flow of water from the hills to the west. After the faulting and the subsequent tilting of the West Coast region there was a diminution in the supply of water to this Ur-Cauvery. The original east-flowing river probably left only a steep-sided wind gap. In addition to the pronounced easterly drainage, the probable presence of a large westerly flowing drainage system with its source very close to the Palghat region seems to be indicated by the landward curvature of the bathymetric contours in the region of the Arabian Sea opposite to the gap and continued WSW to a deep channel, 'the Nine-Degree Channel', between the Laccadive and the Maldive groups of islands. This submarine depression may therefore indicate a submerged river valley. The combined head erosion of these two opposite flowing streams in the Palghat Gap region might have augmented the formation of the low saddle in the gap.

The evolution of the Palghat Gap may be said to have commenced from the time of block faulting of the West Coast and the possible incursion of the sea into the region. This, in all likelihood, took place earlier than the Middle Miocene, and if this surmise is correct, the age of the gap is not later than the Lower Miocene.

Much of this paper is somewhat speculative. If, however, the views put forward, right or wrong, serve as a stimulus for further observations its purpose has been fulfilled.

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The Distribution and Evolution of the Fishes of Palestine

by

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İSTANBUL
1954

The Distribution and Evolution of the Fishes of Palestine [1]

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INTRODUCTION

1. A comparison of the freshwater fishes of Asia and Africa shows how strikingly different these faunas are. Asia possesses a vast number of species and genera of fishes: Africa has less species but a much greater number of endemic families. This basic difference is the result of evolution going on separately in each continent for a long period of changing geophysical conditions. Keeping this in mind we must ascribe a special significance to the few fish families and genera common to both these continents. It is this group of fishes that is the subject of the present study.

The recent connection between Asia and Africa goes back only to the Miocene. Prior to it there was a period of separation. The Tethys Sea spread not only between South Europe and Africa, it continued right to the Indian Ocean. Going back still more we find one African-Asiatic continental complex. Thus, the separation of the continents by the Tethys may be viewed as a mere episode of their history, and the question arises at once whether the faunal elements common to Asia and Africa belong to the earlier period of communication or to the time when a new faunal exchange became possible after the reunion of the continents in the Tertiary. Students of zoogeography and evolution of fishes have shown conclusively that of all the fishes found in both continents a few families only can be referred to the earlier period of junction. The majority are Tertiary intruders (31, 57).

It is natural that much attention has been paid to that region which now represents the continental bridge. Its changing geophysical condit-

[1] This paper, more condensed when read in Istanbul, July, 1951, at the Symposium on Zoogeography of the Near and Middle East, was brought up to date for publication.

ions and climate must have been of decisive influence on the faunal exchange taking place there. Paleogeography has demonstrated that large sections of the Near East countries were submerged in the Tethys which in this region spread from northern Syria to the African continent. The new land bridge, the result of the emergence of these countries from the sea, is thus mainly part of Asia.

How closely the history of Palestine's fauna is tied up with the faunal exchange becomes manifest when one recalls that the strech of land discussed here probably functioned as a continental link supporting migration almost from the moment it emerged from the sea. Whatever existed here of freshwater fishes at the earliest possible date was an invader from outside. Invasion lasted for various and long periods. It was easy at one time, difficult at another. It might not have been continuous. It probably did not start simultaneously at both ends of the bridge. But invasion as such is only the starting point of our story. Invasion could lead to the colonization of the bridge land without leading to transmigration. It might, on the other hand, have resulted in transmigration with no long-lasting colonization. These are only a few instances of what should be considered possible in the complicated chain of events.

Lasting colonization had various consequences. Species could remain uninfluenced by the acquired habitat. Others would undergo more or less extensive changes, giving rise to new systematic entities eventually becoming again the starting point of further migratory activities.

2. Comprehensive collection of systematic and zoogeographic data concerning the freshwater fishes of Palestine began in the second half of the nineteenth century (26, 38, 77). The authors of this early period also attempted to draw a tentative picture of the zoogeographic connections of this fish fauna with that of other countries. Later, additions to the faunal list supplied new material to that trend. BODENHEIMER made contributions to the zoogeographic analysis of the freshwater fishes from an ecological point of view (15, 16).

ARLDT (3, 4) devoted much effort to the clarification of the interrelations of the Asiatic and African fish faunas; special attention was given to the problems of time and routes of the large migratory movements. Some of his conclusions are still accepted. But a better knowledge of the fauna of Asia Minor, advanced largely by investigations of KOSSWİG and his coworkers since the late thirties, made it necessary to abandon part of the assumptions of ARLDT and others. In putting forward a new hypothesis of the history of Palestinian freshwater fishes in 1944 (31) KOSSWIG took advantage of REGAN's broad studies on the distribution of the *Ostariophysi* (57). For the first time also modern geological concepts and the results of zoogeographic research in a broad field was taken into consideration.

The geological development of the Near East was for the first time dealt with in detail on a wide, comparative base in 1943 by PICARD (54)[2]. The geological facts reported in his book and the conclusions drawn from them permit us to follow the history of that particular continental bridge from the Middle Miocene to Recent time. The descriptive sequence of geological stages, though far from satisfactory, is yet the most complete one so far worked out.

During the past decades the zoogeographic aspect of Palestine's freshwater-fish fauna has been enriched by the discovery of a few new fishes (32, 63, 73) and elucidated by the revision of the systematics of others (10. 67, 75).

[2] This study was not yet available when KOSSWIG concluded his 1944 paper

I. PALEOGEOGRAPHY

The arm of the Tethys which united the Mediterranean Sea and the Indian Ocean, while Palestine, Lebanon, Syria, Transjordan, Iraq, and Persia were — partly or completely — submerged, existed up to the Miocene, when it was obliterated by rising land masses. The final stage was preceded by a long series of alternating regressions and by less effective transgressions beginning as early as in the Cretaceous [3]. It appears that ~~that~~ part of West and South-West Arabia was land for an even much longer time; bordering on the one side with the mentioned Tethys arm it was solidly united with the African continent on the other side. From a purely geographic point of view African fauna could thus have colonized Asian territory.. There are no definite paleontological data available to illustrate the actual value of this situation, but it is important to keep it in mind, because the emergence of the Levant countries during the Tertiary is an immensely protracted process. Topographically, it procceeds roughly from south-west toward north-east narrowing the sea to a strait from the Gulf of Alexandrette through Mesopotamia to the Persian Gulf; at the same time, the sea regressed toward west in a front more or less parallel to the recent Levant coast line. Both processes increase the chances for the dispersal of African animals which, by that time, lived in Arabia.

Several stages of the geomorphological development of the Near East countries from the Middle Miocene up to the Plio-Pleistocene transition are represented in the accompanying maps which are either modified and adapted from original sketch maps of Picard (54) or drawn on the base of information found in his book. Many paleogeographic data of the same book were used for the following account.

In the *Middle Miocene* (fig. 1a, b) we find that only a small portion of the Near-East countries has not yet acquired continental character. Marine ingressions cover the North African coastal strip and form bays along the Levant coast the largest of which are the South-Palestine Bay (fig. 1 b) and the deep Gulf of Alexandrette. The vast Mesopotamian basin, only semicontinental at that time, links the Alexandrette Gulf with the Persian Sea. Although the Mesopotamian basin becomes increasingly continental it has probably been an absolute barrier for freshwater fishes during the early stages of its existence; later, it might have been passable for euryhaline species, and slowly became a suitable biotope for a great many fresh-water fishes. In the Egyptian sector the broad continental front is reduced during the Middle Miocene by an ingression of the sea from north-west. Sea water penetrates into the Suez basin which soon is transformed into a semimarine basin. Here, as in the Mesopotamian basin, conditions at first must have been strongly

[3] PICARD (54) remarks: "Land seems to have existed in the higher parts of Trans- and Cisjordan ever since the Upper Eocene" (p. 52). - This, however, does not imply that a continuous mass of land existed there which could be reached by freshwater fishes and which offered conditions sufficient for their survival. It is probable that such conditions developed only gradually during the Lower Miocene.

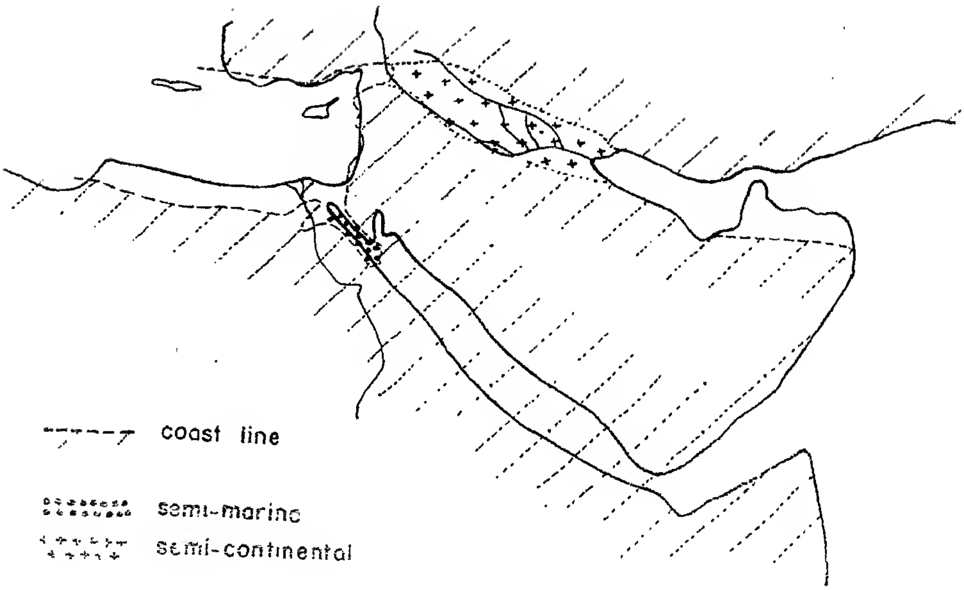

Fig. 1a. Middle Miocene

adverse to the migration of freshwater fishes, but became gradually tolerable for certain euryhaline species. Land as well as freshwater fauna had to resort in their migration to the long southern part of the African-Asiatic juncture.

During the Upper Miocene (fig. 2) geophysical conditions of migration were far better than during the Middle Miocene. The last gap between the Asiatic mainland and Africa (the latter augmented by the Near-East countries), the Mesopotamian basin, was bridged over. Now, certainly freshwater fishes could advance in both directions. — The Bitter Lake region was lifted up and a final barrier formed between the Mediterranean and the Suez basin. Large amounts of freshwater pouring into the closed basin tended to convert it into a freshwater lake. — Most of the coastal strip of Palestine was above sea level.

The Lower Pliocene (fig. 3 a, b) brought an almost complete breakdown of Africa's land connection with Asia: the Erythrean Rift Valley tore open before the waters of the Indian Ocean; the Suez inland basin became a gulf of the Red Sea.—In Palestine (fig. 3 b) deep inroads of the Mediterranean Sea are noted: the Beersheba Bay (with a so far problematic connection to inland basins) and the Jesreel Valley Bay joining south-eastward the large Tiberias inland basin. Several marine inlets are found farther north along the Levant coast.

The history of the inland basins of Palestine and Syria is still obscure in many important details. There are, for instance, reasons to assume that the Miocene Damascus [redacted] comprising Lake Huleh, Lake Tiberias and

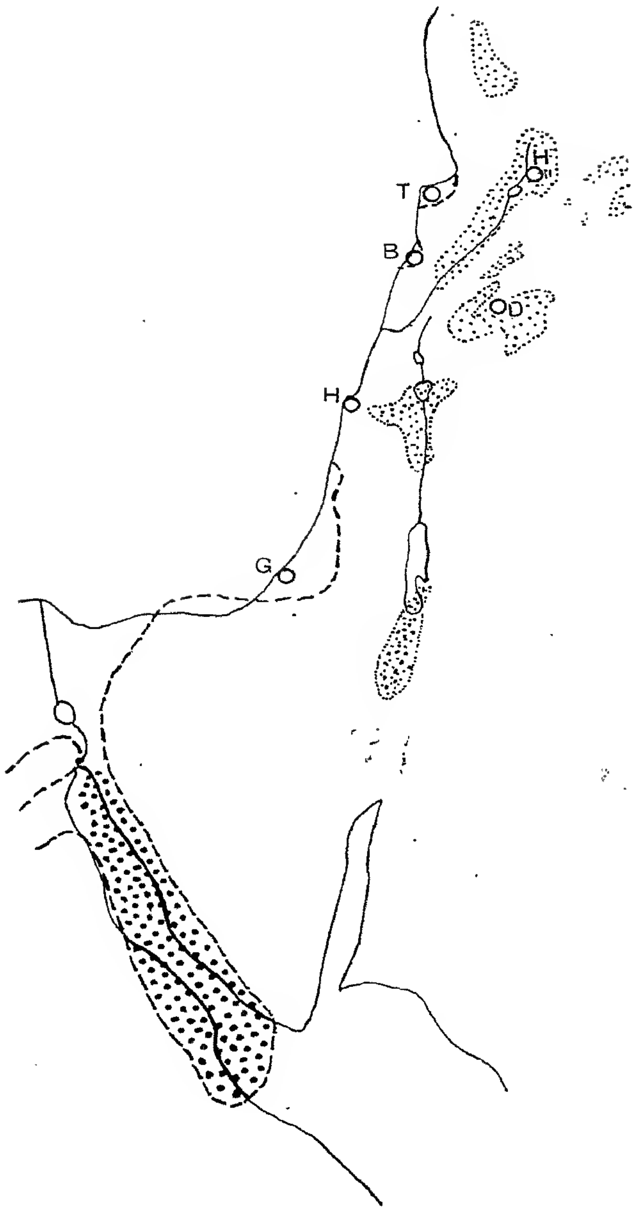

Fig. 1 b. Middle Miocene: Land and water distribution in Suez region, Palestine, Lebanon, and Syria. Fine-stippled: continental basins. G, H, B, T, on the coast: Gaza, Haifa, Beiruth, Tripoli, respectively; D and H inland: Damascus and Homs, respectively.

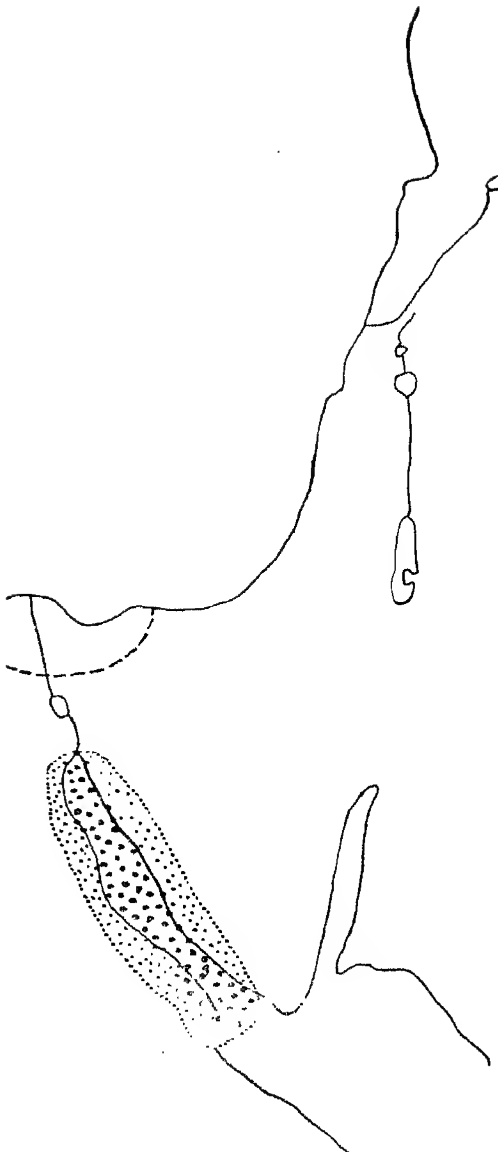

Fig. 2 — Upper Miocene: The Suez region is emphasized, other details omitted. Coarse-stippled : semimarine ; fine-stippled : continental.

the Beth Shean Depression). This is a crucial factor in the migration of fishes. This condition might have lasted until the Upper Pliocene.

There is also no evidence to evaluate the real influence of the Lower Pliocene transgression of the Mediterranean on the freshwater fauna of the East Galilean Basin.

It is by no means clear whether part of these animals had to retreat to rivers draining into the basin or whether shallow bays, strongly flooded by river water, were available as a refuge.

Lake Tiberias and Lake Huleh were united throughout the Pliocene. It is supposed that they are separated at least since the beginning of the Pleistocene (55).

Two continental basins are shown in South Palestine on the Lower Pliocene map (fig. 3b). The western, the Kurnub-Milh Basin, was evidently invaded by the sea coming down through the Gaza-Beersheba Basin. This marine invasion was, however, short termed

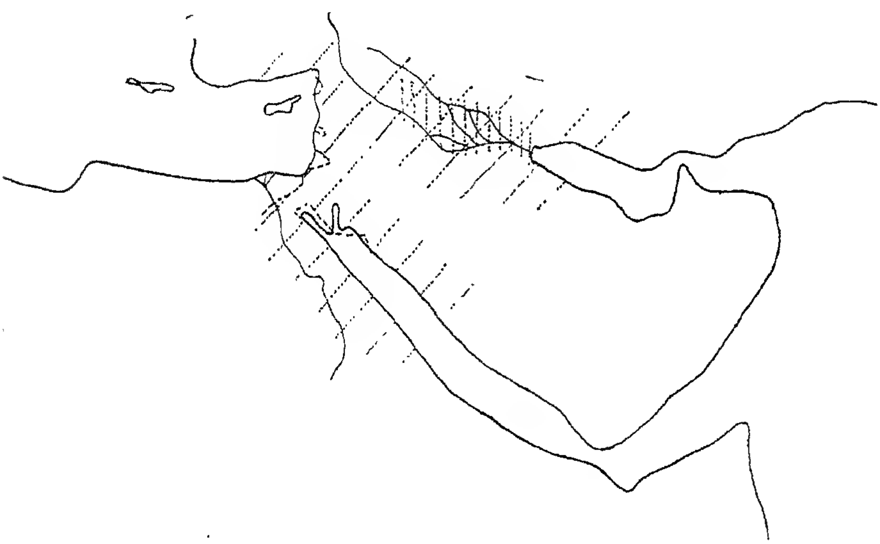

Fig. 3a — Lower Pliocene: The Iraq Basin is indicated by vertical-stippled bars.

and the basin became then purely continental. The eastern basin (Jaib Basin) was part of the Araba Valley. The existence of a communication between the two basins is not beyond doubt. In any event, marine fishes should have been carried far into the land. The lagoonar character of the Kurnub-Milh Basin provided favourable conditions for the conquest of the land by secondary freshwater fishes (42, 43). Whether such an attempt was made and was successful is unknown. As no stringent proof is as yet available for the sea having penetrated farther east (into the Araba Valley), the fossil fishes discovered at Jebel Usdum, south-west of the Dead Sea (PICARD (54), p. 64), gain a key position [4].

It may also be mentioned that nothing in the geological record indicates that the early ingression of the Red Sea into the Aqaba Rift Valley (fig. 5) came up to the Dead Sea.

At the end of the Upper Pliocene (fig. 4) we find the Suez Graben land. Once again migration changes have improved for a comp-

[4] These fishes are not yet studied properly. Their poor state raises doubts as to how far their taxonomic position can be determined. Their age is Tertiary, but no closer determination has been made.

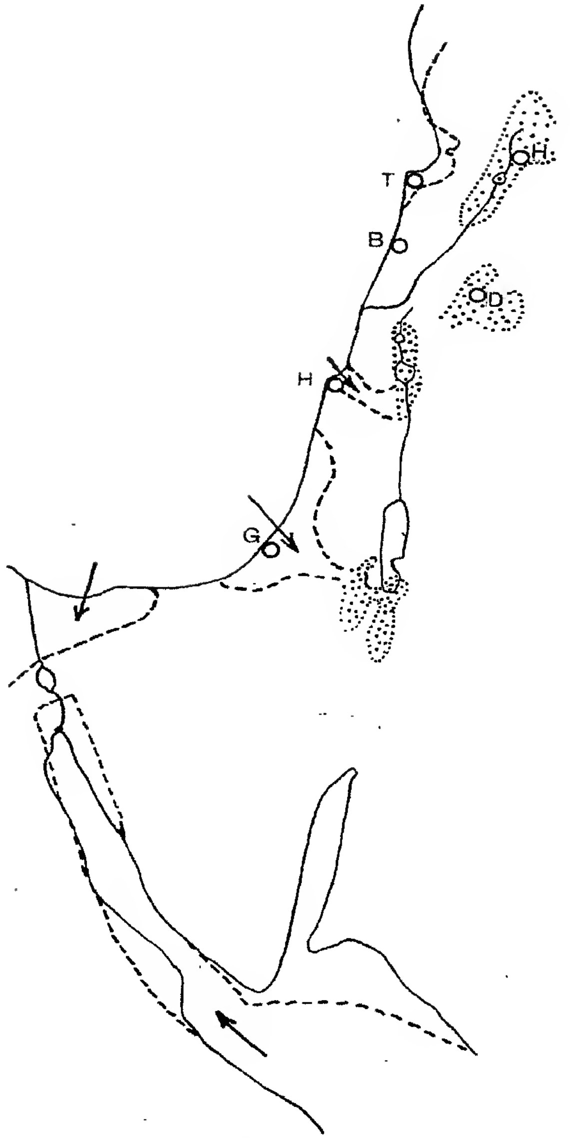

Fig. 3b — Lower Pliocene: Marine ingressions and bays in Suez region and Palestine indicated by arrows.

aratively short time. In the Plio-Pleistocene Transition period (fig. 5) this gain is lost to the Red Sea which renews its ingression into the Suez Basin. Geographic conditions from now on are similar to those prevailing in present time. An uplift of the Isthmus of Suez increases the width of that land junction but is far from making good the loss of the wide Suez Gulf area.

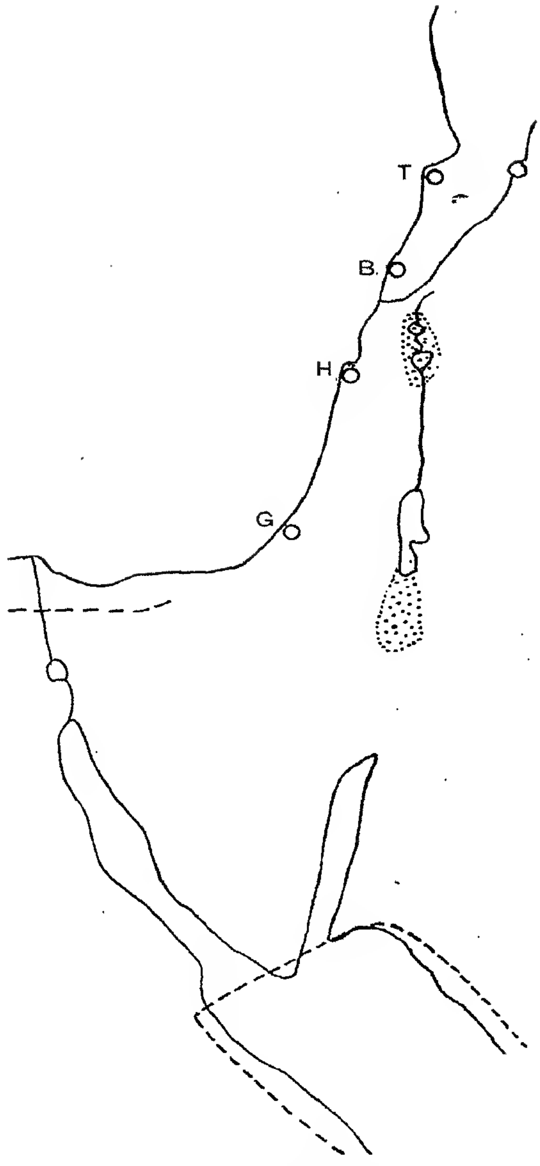

Fig. 4 — End of Upper Pliocene: Coast line represented only in Suez region. Continental basins in Palestine.

The Pleistocene epoch sees many events molding the face of the Near-East countries. Farreaching are the changes in Palestine's landscape. Although the length of time involved is of comparatively low order it is probable, as will be shown later, that evolutionary processes have significantly affected the freshwater fishes during the Pleistocene. However, the faunal exchange between the Oriental and the Ethiopian

Region was probably not longer possible. It was the Tertiary period which determined the general features of the fish fauna of Palestine.

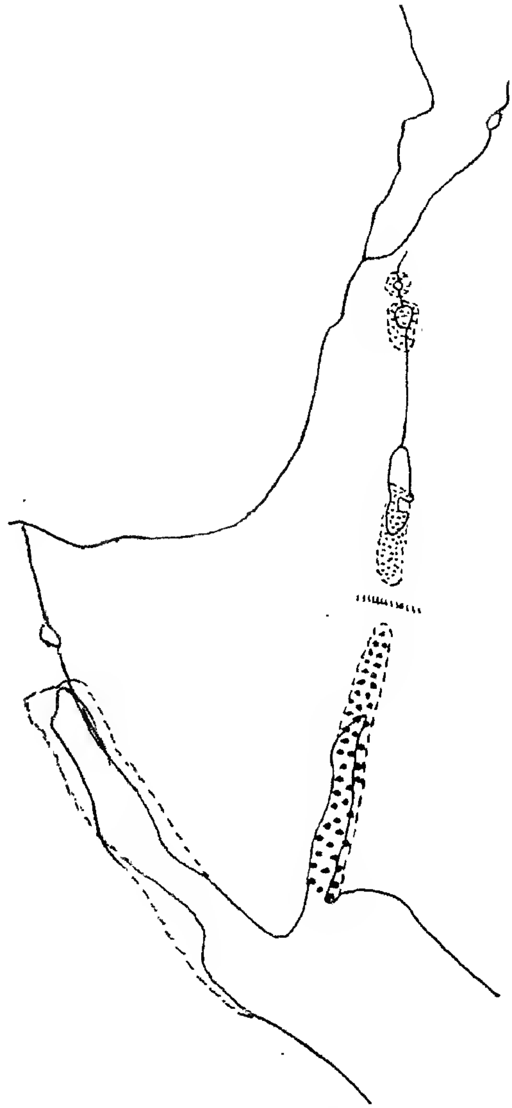

Fig. 5 — Plio-Pleistocene Transition: Suez-Gulf coast line. Aqaba semimarine basin. Arabah water-shed. Continental basins in Palestine.

On the other hand, there is no doubt that the dramatic history of the Jordan Graben in the Pleistocene was accompanied by changes in the distrubution of fishes. Several instances of that kind will be mentioned later.

A variety of distinct types of climate are known to have prevailed at different times during the Pleistocene. But scientists have not yet shown what sort and magnitude of effects fluctuations of temperature and rainfall could have had on the water bodies and their interrelations. An analysis of that kind has only been worked out ~~in~~ for the main section of the Jordan Valley[5]. Yet the upper part of the Jordan Valley and the land west of the main watershed of Palestine pose several zoogeographic problems which can not be solved before more basic work of the geologists is carried out.

II. DISTRIBUTION AND EVOLUTION OF THE FRESHWATER FISHES

1. Cyprinidae

TABLE 1

Cyprinidae: *Origin and Distribution of Palestinian Genera*

Genus	Origin	Recent Distribution	Species recorded from Palestine
1. *Barbus*	S- and/or SE-Asia	Practically all of Asia; Europe; Africa	4
2. *Varicorhinus*	SW-Asia	SW-Asia (Persia and Transcaucasia included); Africa	2
3. *Tylognathus*	S- and/or SE-Asia	SE-Asia; India; Iraq; Israel (Jordan*, Lebanon*, Syria); Asiat. Turkey.	1
4. *Garra*	S- and/or SE-Asia	SE-Asia; Near East to S-Asia; Transcaucasia; S-Arabia; Tropical Africa	1
5. *Acanthobrama*	SW-Asia	Israel (Jordan*); Lebanon (Syria*); Iraq; Anatolia	2
6. *Phoxinellus*	(Central and/or South) Europe	Circummediterranean; "spotty"	1—2

* Countries of probable occurrence, but not actually on record.

Among the six Cyprinid genera of Palestine one is Leuciscine in the strict sense (*Phoxinellus*). Since the zoogeographic history of the Leuciscine division is known to be different from that of the *Cyprininae* it is obvious that the history of the recent Palestinian Cyprinids is rather complex. It should also be noted from the onset that the

[5] Special references to this problem see in the bibliographic list of PICARD's paper (54).

most primitive division of the *Cyprinidae*, the Bariliine group, is not represented in Palestine, although it is existing in the Near East and Africa. Thus, a first classification of the *Cyprinidae* opens a view of the intricate development of the family in the region discussed.

TABLE 2

Cyprinidae: *Distribution Pattern of Palestinian Species*

Genus	Species	Distribution
1. *Barbus*	*canis*	Syro-Palestinian
	longiceps	Syro-Palestinian
	continii	Endemic
	beddomi	Endemic
2. *Varicorhinus*	*damascinus*	Anatolian-Syro-Palestinian
	sauvagei	Endemic
3. *Tylognathus*	*steinitziorum*	Endemic
4. *Garra*	*rufus*	Syro-Palestinian
5. *Acanthobrama*	*terrae-sanctae*	Endemic
	lissneri	Endemic
6. *Phoxinellus*	*kervillei*	Anatolian* — Syro—Palestinian
	(*zeregi*)	(Syro-Palestinian)

Endemic	6	species
Syro-Palestinian	3—4	species
Anatolian-Syro-Palestinian :	2	species

* Courtesy Prof. KOSSWIG, İstanbul

The genus *Barbus* is still most abundant in its region of origin [6], the Oriental Region. From Palestine four species are reported.

B. beddomi GÜNTHER (26) and *B. continii* VINCIGUERRA (78) have both a single record in the literature. It is not impossible that their geographic range is even restricted to part only of the Jordan system as both were caught in Lake Tiberias; but no conclusive evaluation is possible at the present time. Systematically, *B. beddomi* belongs to the large-scaled species of the genus (28 scales in the long. line) as does *B. canis* C. V., another species of Palestine. It is to be regretted that no detailed account of *B. beddomi* has ever been published;

[6] The problem of a more accurate localization of the evolutionary focus of the *Cyprinidae* is treated in considerable detail by HORA in several papers. His argument points to South-East Asia rather than to Central Asiatic regions favoured by earlier authors (see HORA: 1937, Curr. Sci. Bangalore, 5 (7): 351-356; 1938, Proc. Nat. Inst. Sci. Ind., 4 (4): 395-409; 1938, Curr. Sci. Bangalore, 6 (8): 370-372.).

GÜNTHER's short report is no base for comparing the species with *B. canis*. We are in a slightly better position with regard to *B. continii*, for VINCIGUERRA (78) points to the great similarity of the latter with *B. canis*. Yet we are not sure of the taxonomic significance of this species' scale count; the single value of 42 may well be above the still unknown mean. *B. canis* has a mean scale count of 33.4 with a range of 31—36[7]. Of *B. canis* a few records are published from Homs and Antiochia (24, 38). In the Lebanon and Syria more members of the genus are found; it would be interesting to consider the kind of relationship existing between the Palestinian species and those living in the countries north of Palestine. Unfortunately no study of that sort has ever been published. It is, however, safe to assume that both the large-scaled and the small-scaled *Barbus* species were developed early in the home land of the genus; both are well represented today in Africa as, indeed, they are in the Oriental Region and in the Near East. Beyond this general statement, some information of a more particular character is available. TREWAVAS (74) in studying the Arabian *Cyprinidae* described the new species *B. arabicus* and, searching for its relatives among the species of the genus, stated that *B. canis* appears to be the closest ally. Among the African large-scaled *Barbus* none was indicated by TREWAVAS as especially near to *B. arabicus*, but among the Indian species *B. tor* (HAM.) and *B. putatoria* (HAM.) are marked in that respect. Taken for granted that *B. tor, putatoria, canis*, and *arabicus* are related with each other in the way stated by TREWAVAS, it is clear that this reflects in a certain manner the geographic position: *B. canis* and *arabicus* are very closely allied; they are separated by a distance which is small when compared with the distance of Arabia or Palestine from India, where *B. tor* and *putatoria* live both of which are taxonomically less close to either of the Near-East species. We do not propose any hypothesis concerning the particular descendance of the group since the four species have not been studied from that point of view; but it is evident that the situation discussed here is well in favour of the argument submitted in this paper[8].

We can not offer anything similar with regard to *B. longiceps* C. V. The only record of this species outside Palestine is from Homs, Syria (24). Its geographic range is more limited than that of *B. canis*. With an average scale count of 55.7[9] it belongs to the small-scaled group of the genus which occurs in Asia, Africa and Europe. Beyond this we do not know anything of its special systematic interrelations.

Only two species of the genus *Varicorhinus* are assumed to occur in Palestine (69). Both of them are not easy to evaluate — each in a different sense. *V. sauvagei* (LORTET) (38) is one of the species not

[7] 21 counts in specimens from Lakes Tiberias and Huleh (unpublished data, A. BEN-TUVIA and H. STEINITZ).

[8] KOSSWIG's (31) conclusions concerning the same problem were different.

[9] The mean of 29 specimens from Lakes Huleh and Tiberias, with a range of 51-60 (unpublished, A. BEN-TUVIA and H. STEINITZ).

only considered endemic in Palestine, but possibly restricted even to the Jordan Valley. The specimen on which LORTET founded this species was caught in Lake Tiberias. Additional animals of the species have not been secured. No reexamination of it was ever published. Thus, we have to resort entirely to what facts are reported in the original description. Three of the characters mentioned are of importance for defining the position of the species. It has one pair of barbels, large scales (33 in the long. line), and the lateral line incomplete, running over 7 scales only. The large-scaled species among those named today *Varicorhinus* RÜPPELL were included by HECKEL in his genus *Dillonia*, an African group. The great majority of the African species, now attributed to *Varicorhinus*, possesses large scales while the Asiatic species are for the greater part small-scaled. The alliance of *V. sauvagei* with African representatives was realized by LORTET himself; he placed the species near to *Capoeta Dillonii* C. V. (= *V. beso* RÜPP.) from Abyssinia, and VINCIGUERRA (78) pleaded for its inclusion in *Dillonia* for the same reason. GÜNTHER (25), while not recognizing *Dillonia* as a separate genus, still gave weight to the scale size of the species and compromised on *Dillonia* in subgeneric rank. BOULENGER (18) abandoned the rule of scale size: in his systematic key scale size and number of barbels are given equal roles. The wisdom of this measure is to be doubted. The information available clearly shows that the two characters can not be used concurrently in the whole of the genus. On the other side, from the analysis of numerous Cyprinid genera we learn that scale size seems to be the more constant of the two characters. We conclude, therefore, that the number of barbels does not interfere with the systematic relation of *V. sauvagei* (as also of some other Asiatic species) with the large-scaled African species. But we should also consider a close connection of *V. sauvagei* with another small group of fishes for which PELLEGRIN (50) created the genus *Hemigrammocapoeta*. Briefly stated *Hemigrammocapoeta* is a large-scaled *Varicorhinus*-like genus distinguished by an incomplete lateral line. The type species, *H. culiciphaga* PELLEGR., has 29—32 scales. *H. kemali* (HANKO) (= *V. kemali* HANKO) (27) has 37—40 scales. *V. sauvagei* must be reexamined in order to decide whether it should also be ascribed to *Hemigrammocapoeta*: as mentioned its lateral line is incomplete, its scale count is 33 (from this figure it is fairly sure that the specific scale-count range does not ingress that of the small-scaled group). Whether *Hemigrammocapoeta* merits generic standing or not is of minor importance, for in any case the systematic situation leads to the conclusion that the fishes constituting this category are descendants of the large-scaled *Varicorhinus*. Wether *V. sauvagei* branched off the main stem along with *Hemigrammocapoeta* is a point for further study. In the latter event *Hemigrammocapoeta* would inhabit an area from Asia Minor down to Palestine.

V. damascinus C. V. has a wide distribution area covering Asia Minor, Syria, Lebanon, Palestine and Transjordan, probably also Iraq,

part of Persia and Transcaucasia. The growing knowledge of the freshwater fishes of the Near East changed the status of *V. damascinus* considerably. Several *Varicorhinus* forms, often listed as distinct species, must be included in *V. damascinus* as has been pointed out by KOSSWIG (34) and STEINITZ (69). KOSSWIG demonstrated the geographic grouping of populations with overlapping scale-count ranges of 52-99. He draws *V. capoeta* HECKEL, *peregrinorum* HECKEL, *umbla* BATTALGIL, *capoeta* HANKO, and others to the species *damascinus*. He also considers the inclusion of *V. syriacus*. STEINITZ showed that *syriacus* is not separable form *damascinus* for various reasons. All these data are sufficient to make a revision of *V. damascinus* desirable. It may be said that probably several groups will ultimately be recognized, defined not only by the scale count but by other characters as well; but, as far as the analysis has shown, the taxonomic redistribution will not coincide with the earlier species now comprised within *damascinus*. However, on the base of present knowledge the following remarks may be made concerning the geographic implications of KOSSWIG's concept. The range of scale counts (total range: 52-99) of the individual groups varies from 3 to 26 scales[10]. We have no information of the area inhabited by the respective populations, nor of the variability of ecological conditions. But it is in accord with zoogeographic rules to find that the total range represented in as vast an area as Asia Minor is by far larger than that of any single geographic group. This is born out in our case by the difference of 47 between the lowest and the highest count. It is also in compliance with this rule that TORTONESE (71) finds a range of 9 scales (68-77) in 103 specimens from an area roughly outlined by the Mediterranean coast in the West, the Lake of Homs (Syria) in the North, Es Sanamein (Syria) and Rabbat (Amman, Transjordan) in the East, and Jericho (Palestine) in the South. A sample of 10 specimens from Lakes Huleh and Tiberias had a range of 15 (67-82)[11]. Since the data from the Syro-Palestinian zone have been obtained from fairly well spaced samples it may be presumed that future investigation will not change the range by more than ± 5 and, consequently, not bring it close to either side of the total range of Anatolia. Although more information remains to be collected, from that we have at present, the impression is gained that the total scale range of Asia Minor may be close to the total scale range of the species as a whole. The importance of the minimum value is at once clear if it is interpreted as the genetically fixed limit beyond which development would normally not go. *V. damascinus* reaches lower scale counts than any of the other small-scaled species. But none of the large-scaled ones reaches up to them[12]. This should reassure us in the view that small- and large-scaled

10 The low value could be caused by a small sample; size of samples is not recorded by KOSSWIG.

11 Unpublished data, A. BEN-TUVIA and H. STEINITZ.

12 It is noteworthy that BOULENGER (18) incidentally set the limit at 40 scales which would still hold good regarding recent knowledge.

species represent different lines of evolution. Since both of them occur in Africa (see above), we are compelled to assume that early large-scaled and early small-scaled *Varicorhinus* migrated from Asia to Africa. In other words scale size differentiation in two different directions has set in early in the history of the genus. We shall return to this aspect of the problem later.

Barbus and *Schizothorax* appear to be closer allied to *Varicorhinus* than any other Cyprinid genus (*Hemigrammocapoeta* is, of course, excepted from this statement). *Barbus*, it may be assumed, is the more primitive of the two indicated; it is also less differentiated than *Varicorhinus*. In addition, it has a vast distribution. *Schizothorax* is limited to Central and Western Asia (with one species extending into Anatolia); *Varicorhinus* is limited to the Asiatic area specified in Table I but occurs also in Africa. It is not likely that *Schizothorax* belongs to the ascendance of *Varicorhinus*, but it is, on the other hand, not improbable that *Barbus* (or a still more primitive extinct genus) is a parental form of both, *Varicorhinus* and *Schizothorax*. There is nothing in the geographic distribution of *Varicorhinus* suggesting that its home has been in South and/or South—East Asia. Besides, such a view would imply that there as well as in the zone between the alleged home and the recent living area it became extinct. Paleontology does not supply any relevant information.

One might perhaps think of the possibility that the Iraq Basin (PICARD (54), p. 54 and 72) offered a wide variety of conditions for tropical fish to thrive and differentiate. When the last remnant of the Tethys Sea that was capable of halting the invading fishes from the East, closed during the Miocene it was replaced by what is called the Iraq Basin. The low Mesopotamian Gulf transformed into a lagoonal basin into which rivers incessantly poured their waters. Slowly the basin changed from semi-marine to continental. River deltas, a growing marginal belt of freshwater and an increasingly deep layer of fresh surface water must have formed a huge central body interrelating river systems of opposite sides. Some of the incoming fishes may have left it sooner, others stayed for various lengths of time. To them evolution offered many chances. In any event, arrival of new elements and departure of earlier ones were long-lasting and, in part, simultaneous processes. Although changes were in all probability more farreaching when migrations were interrupted for longer periods, it must be kept in mind that later-on continuation of the travel in any direction became difficult. In this as in adjacent territories the climate turned drier; the water volume shrank, salt deposits accumulated; more and more barriers to easy life were the result of growing aridity. The turn for the worse must have stimulated adaptive capacities. But it seems probable that at the same time a heavy decline of the fish population followed in the wake of the events mentioned. The survivors, a relict fauna in a certain sense, are found in the Near-East countries where they have further spread, split up geographically and systematically, and adjusted themselves to new surroundings. *Varicorhinus* may be one of the many evolved in the Iraq Basin and one of the few spared from extinction. Of the relicts existing in the Near East this genus is certainly one of the most successful.

In the light of these speculative considerations several phylogenetic developments mentioned earlier can be correlated in time and space. The splitting of the young *Varicorhinus* stock into two main branches, the one large-scaled, the other small-scaled, must have occurred early and within the center of origin; for both are represented in both the Asiatic and the

African area of the genus. In Asia speciation resulted in numerous species, particularly on the small-scaled line, most of them inhabiting Anatolia. On the large-scaled line Asia was less productive than Africa, but a new side branch was raised in Asia, keeping the large scales but reducing the lateral line: *Hemigrammocapoeta*.

The presence of *Varicorhinus* in the Iberian peninsula suggested by BERG (13) is highly doubtful. It has never been confirmed by ichthyologists on the spot or elsewhere. However, from a zoogeographic point of view the alleged area could have been colonized from Africa Minor during the Pleistocene when a land bridge was in existence in that region between the two continents concerned. Today, Africa Minor has only one species, *V. maroccanus* (GTHR.). The majority of the African species are living in the streams and lakes of the tropical part of the continent. The recent species of the Asiatic Near East, as apparantly also *V. maroccanus*, represent an ecological type different from that of tropical Africa. Although they may thrive in large water bodies, several, if not the majority, are capable of living in streamlets and brooks with extremely varying conditions: rapid, torrential winter and spring currents turning into scanty, trickling streamlets in which the almost stagnant water is readily heated during sunny days.

In a preceding paragraph we remarked that *Varicorhinus* might have originated in large tropical water bodies. The species of tropical Africa are of an ecologically similar type, but it is questionable whether they simply continue on the line of an ancient adaptation. KOSSWIG repeatedly pointed out that the Asiatic invaders encountered increasing arid conditions as their migration went on. Surely, the earlier the emigrants started out, the less had they to adjust to worsening conditions. Nontheless, we were in favour of a certain retardation of the migration to allow for the differentiation of two main branches. The assumption of this differentiation taking place prior to immigration is prerequisite to understanding the present situation in Africa and the Near East. Considering the extensive speciation of *Varicorhinus* in the Near East, particularly in Anatolia, KOSSWIG (34) prefers early spreading from the development center and early immigration into Anatolia. It should be pointed out that "retardation" of emigration in the one, and "early" immigration in the other, argument are not necessarily contradictions.

Successful adaptation to water conditions in semi-arid countries and to subtropical and even lower-rating climates is another aspect of the speciation process. We do not agree with KOSSWIG (34, p. 97) when he asserts that the spawning of Anatolian *Varicorhinus* in the late spring, when the water is warm, points back to the tropical origin of the genus or expresses thermophily. We rather prefer to see in this conduct one of the many signs of the remarkable adaptability of the genus. *V. damascinus* is spawning in the Huleh district (Palestine) in late February and March when it enters the high running wadis in big shoals. The water is at that time very cool, indeed. But in May these wadis would be more or less dry. A subtropical though semi-arid

country may, as we see, compel a fish to spawn in cool water if it requires current water for reproduction.

The genus *Tylognathus* has become well known in the Near East during recent years. Since 1938 four new species were described (32, 71). Of them *T. steinitziorum* KOSSWIG is the only representative of the genus within Palestine. There, it has been found in the Jordan System only. The interrelations of all the Near-East species will be more conveniently appreciated if their discussion is preceded by a short statement about the genus as a whole.

India and South-East Asia (including the Indo-Australian Archipelago) comprise the main area in present time. Altogether six species are known from the Near East. The genus is not reported from the intervening countries. No *Tylognathus* is reported from Africa. This situation points to the Oriental Region as its early center. Since *Tylognathus* is a very typical representative of Near East fishes it is useful to compile such information as is available from various scattered sources. The map (fig. 6) will help in visualizing the distribution pattern

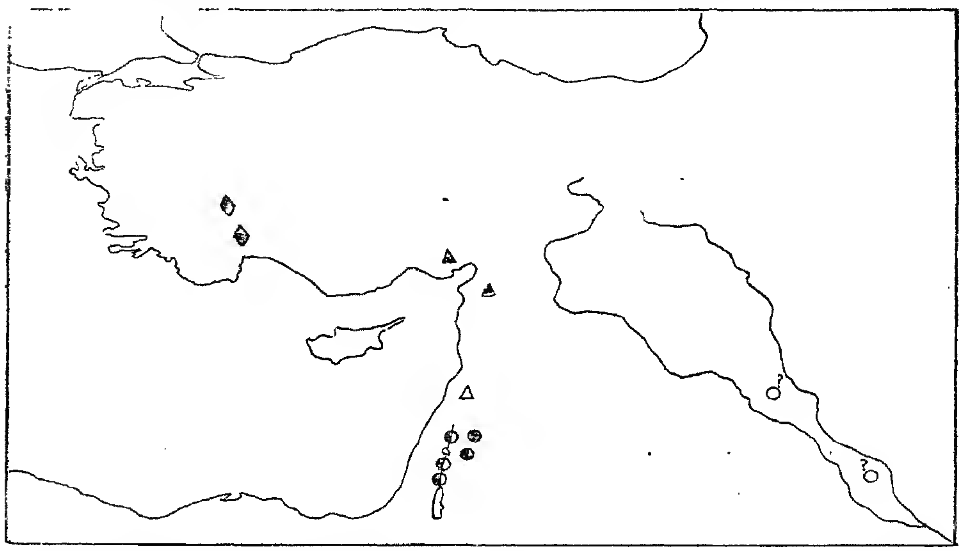

Fig. 6 — Distribution of *Tylognathus* in the Near East. Subgenera: *Tylognathus* s. str.: circles; *Tylognathoides*: triangles; *Neotylognathus*: upright squares (same symbols as used in fig. 7).

- ● *T. nanus*;
- ◐ *T. steinitziorum*;
- ○ *T. elegans* (localities undefined, distribution questioned, see text);
- ▲ *T. caudomaculatus*;
- △ *T. festai*;
- ◆ *T. klatti*.

of the subgenera; for the sake of a more accurate picture it is supplemented by the following list of localities recorded for the various species.

Tylognathus (Tylognathus) elegans GÜNTHER: "Mesopotamia?" (Iraq) (25).
— — *nanus* HECKEL: Barada River, Damascus, Mzerib (Syria) (28, 49, 71).
— — *steinitziorum* KOSSWIG: Jordan System (Palestine) (32, 69).
— *(Tylognathoides) festai* TORTONESE: Schtora (Lebanon) (71).
— — *caudomaculatus*[13] (BATTALGİL): Ceyhan System; Hatay (Asiatic Turkey) (6, 32).
— *(Neotylognathus) klatti* KOSSWIG: Gölcük Gölü; Eğridir; Büyük Menderes (7, 32).

The distribution of this originally tropical genus in non-tropical and predominantly steppic areas is, as the map shows, sporadic. *Tylognathus* appears as a relict in a region where conditions today are far from tropical. The speciation process which resulted in physiological adaptations to the new habitats left its marks also in structural characters that can be used with advantage in the systematics of the genus in the region discussed.

Tylognathus is described as possessing barbels and a complete lateral line. The species *elegans*, *nanus* and *steinitziorum* confirm this definition. The species *festai* has an imcomplete lateral line, but is otherwise in good agreement with the definition of the genus. Therefore, TORTONESE created the subgenus *Tylognathoides* to include *festai*. KOSSWIG assigned the species *caudomaculatus* whose lateral line is also incomplete, to the same subgenus. *T. klatti* is another species with the lateral line incomplete, but in addition distinguished by the lack of barbels. For that reason KOSSWIG established the subgenus *Neotylognathus* which is monospecific as far as our present knowledge goes. Table 3

TABLE 3

Subgenera of Tylognathus

Distribution of Taxonomic Characters

Lateral Line / Barbels	Complete	Incomplete
present	*Tylognathus s. str.*	*Tylognathoides*
wanting		*Neotylognathus*

summarizes the distribution of the relevant subgeneric characters in the genus. The accompanying diagram (fig. 7) illustrates the possible appearance of these distinctive peculiarities during evolution. The implied assumption corresponds well with the geographic distribution of the subgenera, see fig. 6. Briefly outlined the geographic and differentiative progress of the genus in the Near East could well have been as follows:

[13] Synonym: *Hemigrammocapoeta caudomaculata* BATTALGİL (6).

the evolution center of the Near-East species is to be looked for in the Mesopotamian Basin. If the occurrence there of a *Tylognathus s. str.*

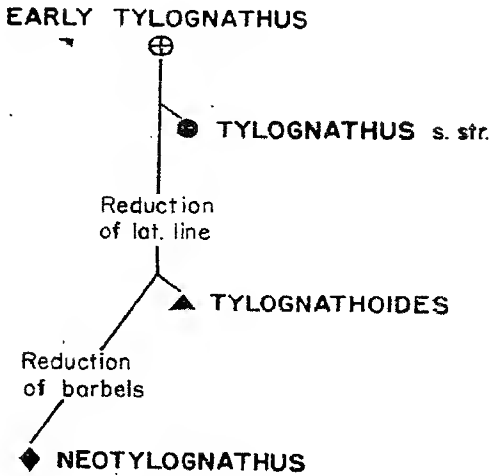

Fig. 7 — Diagram of hypothetical branching of subgenera of *Tylognathus*. (Symbols same as in fig. 6).

(*T. elegans*) could be confirmed, another piece of evidence might be on hand. *Tylognathus s. str.*, represented by *nanus*, is reported from Syria, and very close to it, another member of the subgenus is on record: *steinitziorum* from Palestine. *Tylognathoides* went farther in differentiation by reducing the lateral line. So far, this subgenus is reported as *festai* from Lebanon and *caudomaculatus* from places north and northwest of the latter. The last differentiative step was taken by *Neotylognathus* in eliminatig also the barbels: *klatti* is found farthest to the north and west.

Garra rufus (HECKEL) is the only representative of the genus in Palestine, but is also noted from Jordan, Lebanon, Syria, South-East Anatolia and Iraq[14] (14, 24, 28, 35, 71). *G. variabilis* (HECKEL), although found in an area largely overlapping with that of the former species, has never been reported from Palestine (28, 35, 60).

Since *Garra* is an oriental genus which succeded in colonizing large parts of Africa, it is important to consider the systematic position of *G. rufus* within the genus. In doing so we follow closely HORA (29) who has made a special study of *Garra*. According to him the trend of evolution of the species is marked by the structural change of the air bladder. Based on this character groups of primitive and of more or less specialized species are recognized. *G. rufus* belongs to the prim-

[14] South-East Anatolia and Iraq are omitted in Table 2, but this does not change the overall distribution pattern.

itive group, as does *G. variabilis*[15]. Those species of the primitive group which have a special interest for our problem may be listed here:

G. lamta BUCH. HAM.: India.
G. rossicus (NIKOLSKY): Persia, Afghanistan, Baluchistan.
G. rufus (HECKEL): Near East.
G. variabilis (HECKEL)[15]: Near East.
G. blanfordi (BOULENGER) Abyssinia.

The distribution of this group is roughly illustrated in the map (fig. 8: circles). There, two more species belonging to the same group are shown: *G. tibanica* TREWAVAS and *G. brittoni* TREWAVAS, described as new species from South-West Arabia in 1941 (74). Analyzing the taxonomic relations of the Arabian species TREWAVAS pointed out that *G. tibanica* and *brittoni* are most closely allied with *G. blanfordi*; moreover, the alliance is so close that they are perhaps only subspecies of the latter. TREWAVAS also reports of an unnamed *Garra* species from British Somaliland, also very similar to the former species. *G. aethiopicus* (PELLEGRIN) from Abyssinia is assigned to the same group. None of the other Asiatic species, TREWAVAS declares, is as near to the said group as the group members are to each other. This situation can hardly be interpreted otherwise than as the result of development from an ancestral *Garra* of the primitive group which occupied a continuous area. When geological events disrupted the connection and separate populations were created speciation produced the taxonomic entities found in the present geographic position. This hypothesis is not in contradiction to the paleogeographic developments reported. The Red Sea formed in the Lower Pliocene; in the Upper Miocene South Arabia was united with Africa. The migration of oriental fishes reached the Near East during the Miocene when the Iraq Basin became continental. It had brought primitive *Garra* species which spread to the Near East, where they are represented today by *G. rufus* and *variabilis*, and via Arabia to East Africa. KOSSWIG commented on the distribution of *Garra* in his paper of 1944 (31), p. 69—70, but came to different conclusions. He was not aware that a closer relation exists between the *G. blanfordi*- and the *tibanica*-group and the Near-East species. He cited TREWAVAS as saying that *G. tibanica* and *G. lamta* have many features in common, but failed to recognize the close relation between *G. lamta* and *G. rufus*. As mentioned above, HORA attributed *G. lamta* and *rufus* and, implicitly, *G. variabilis*, to the primitive group within the genus. TORTONESE (71) showed in detail that *G. rufus* and *lamta* are practically indiscernable; recently STEINITZ (69) came forward in support of TORTONESE's opinion. Thus, present day knowledge of the primitive *Garra* species combined with that of paleogeography of the Near East-Africa region enables us to present a hypothetic outline of the history of those species in their migration from the Oriental to the Ethiopic Region.

[15] By virtue of its close alliance with *G. rossicus*, l. c.

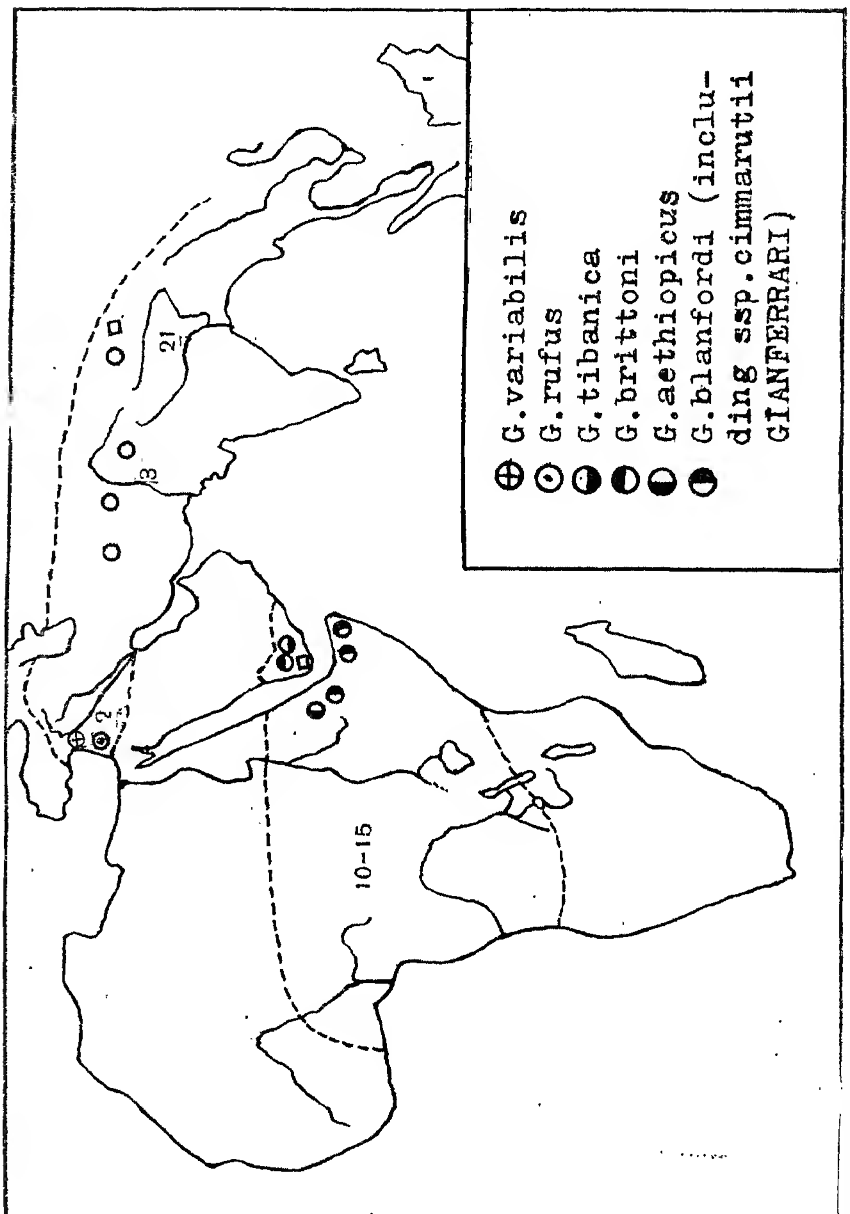

Fig. 8 — D i s t r i b u t i o n o f *Garra*. The distribution area is roughly outlined. The number of species supposed to occur in each of the following areas is indicated: Borneo; Continental South and East Asia; Balutchistan, Afghanistan and Persia; Near East (Arabia excluded); Africa. Primitive (circles) and specialized (squares) species are particulated in the Near East, South-West Arabia and the area of Africa opposite South-West Arabia. For more details see text.

Less satisfactory is the situation with regard to the specialized *Garra* species. While they are well known from present-day India they are absent from the Near East except South-West Arabia. *G. arabica* HORA (29) was described from a locality near to those of the two Arabian species mentioned above. HORA says that this species is closely related to *G. stenorhynchus* (JERSON) and *gotyla* (GRAY). All three of them belong to the most specialized group of *Garra* as demonstrated by their air bladder and other common characters. We should therefore assume that the specialized parent of *G. arabica* joined the primitive *Garra* species in leaving the Oriental Region for Arabia. TREWAVAS comments that the presence of this "specialized Indian section of the genus" in South—West Arabia is surprising. If it is assumed that at the time the west—bound migration started, the oriental *Garra* had already given off primitive and specialized groups, the occurrence of a specialized species in Arabia requires no explanation different from that suggested in connection with the primitive species. It is not known whether all the African *Garra* species are members of the primitive group. HORA himself examined only *G. blanfordi*, and we know of no report on corresponding studies with regard to the remaining species so far described[16]

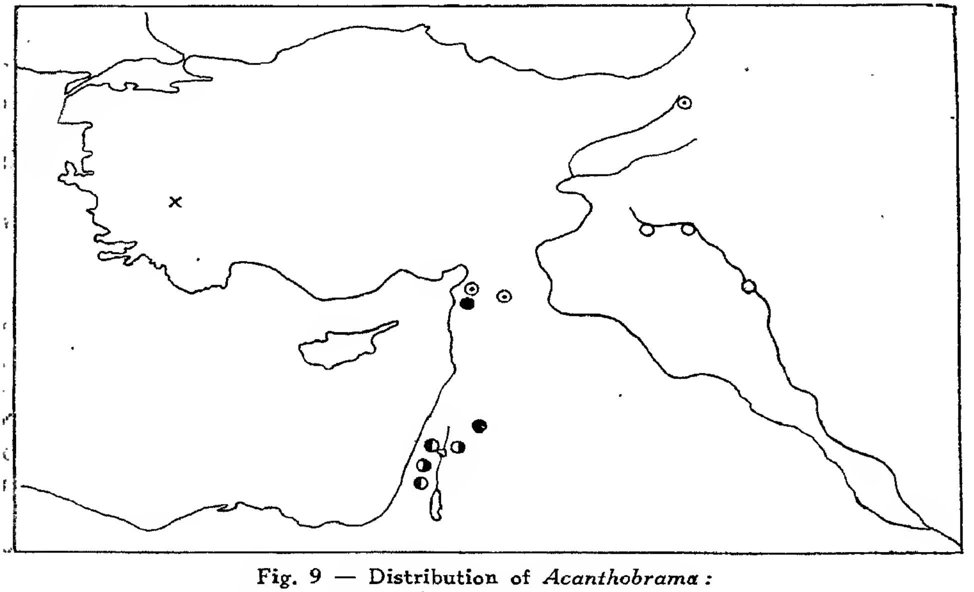

Fig. 9 — Distribution of *Acanthobrama*:

⊙ *A. marmid* (= *cupida*), incl. ssp. *orontis* BERG;
● *A. centisquama*;
○ *A. arrhada*;
◐ *A. terrae-sanctae*;
◑ *A. lissneri*;
× *A. spec.* (not named, see KOSSWIG, 34, p. 87).

16 About 10—12,1. c.

(18, 41). The application of HORA's principles to a broad comparative-anatomical study of the African species is supposed to help elucidating the connection between Asiatic and African species of *Garra*.

Acanthobrama is a small genus, both, in area occupied and in number of species. About five species are described, two of them, *A. lissneri* TORTONESE (73) and *A. terrae-sanctae* STEINITZ (67), from Palestine. The occurrence of another species in Palestine has been denied (69).

The two Palestinian species are closely allied to each other. *A. terrae-sanctae* has been said to be near to *A. cupida* (HECKEL) (67). On the other side *A. cupida* and *A. marmid* HECKEL are difficult to separate, so much, indeed, that TORTONESE (73) sees in *cupida* but a synonym of *marmid*. *A. arrhada* HECKEL seems also to be fairly close to *marmid*. *A. centisquama* is less near to all the other species mentioned. The Anatolian *Acanthobrama* mentioned, but not specifically named by KOSSWIG (34), can not be discussed here.

It may be useful to have the localities of the various *Acanthobrama* species tabulated in the following list.

A. centisquama HECKEL: Damascus (28), Antakaya (35).
A. arrhada HECKEL: Mossul (28), Diyarbakır, Batman suyu (35).
A. marmid HECKEL (= *cupida* HECKEL), including *A. marmid orontis* BERG (14): Aleppo (28); Erzurum (73); Antiochia-Orontes (14).
A. lissneri TORTONESE: Jordan System (73); coastal rivers in Palestine (unpublished).
A. terrae-sanctae STEINITZ: Jordan System (67): coastal rivers of Palestine (unpublished).
A. spec.: Grosser Maeander (fide KOSSWIG (34), p. 87).

The genus is not known from anywhere but the places listed above. But extensive exploration of Syria, Lebanon and Jordan may reveal more localities in the Near East and help settling the confused geographic situation illustrated by the map (fig. 9). It is also necessary to learn whether *A. arrhada* or any other species are existing in the lower Tigris and Euphrates. KOSSWIG (34) pointed out that Central Anatolia is not inhabited by the genus which, however, is found in the Egean marginal zone of South—West Anatolia. TORTONESE in adding Erzurum to the localities of *A. marmid* markedly enlarged the area of the species. A significant geographic link might be discovered in this locality, for *Acanthobrama* is held most nearly related to *Capoetobrama* BERG [16a] ‡ which is known to occur in the Aral System (l. c.). This relationship — if true — is, by itself, not indicative of the place of origin of *Acanthobrama*. The largely Palestinian-Syro-Anatolian distribution of

[16a] BERG created the genus *Capoetobrama* to include the only species *C. kuschakewitschi* (KESSLER) which until that time had been assigned to *Acanthobrama*. See: BERG, L. S., Les poissons des eaux douces de la Russie, Moscow, 1916 (p. 316-318); Russian.

the present time is no proof that the development center was in the South-West part of that area. If one believes that ecological features can be of use in reconstructing the past, spawning during the cool months of the year could be taken as clue of a more northern origin. At present we know the spawning season of *A. terrae-sanctae* and *A. lissneri* only. The reasoning mentioned is naturally valid only if other species of the genus fit into the premisses indicated. The question should be studied from various angles whether an immigration of *Acanthobrama* in the wake of Pleistocene glaciation into the south-west of Central Asia could have been possible from somewhere at the border of Central and South-West Asia. In late Tertiary times the lower land level of Anatolia, its big rivers and the central Anatolian lake system furnished ways of communication between North-East and Central Anatolia and between the latter and Syro-Palestine (34, 36, 39, 59). If they aided *Varicorhinus* in reaching Anatolia and even Transcausasia [17], they could have been eminently effective in the spread of *Acanthobrama*, in the opposite direction, during the Pleistocene when (and as much as) a more humid climate was dominant. Increasing dryness had naturally fatal effects: reduction of the population, dissection into separate units and restriction to much fewer biotopes isolated by bigger distances. The small number of species (less than the perhaps much older *Varicorhinus* has) would also be a factor in support of the younger, post-Tertiary age of this genus. The fact that *Acanthobrama,* although living in the Egean region of South-West Anatolia, did not reach Europe via the Egeopotamos is not necessarily in favour of the hypothesis submitted here. It is true that a late post-Tertiary immigrant could have found the Egean continent broken down when he arrived there (34, 73). But it can be argued equally well that it was the "West-Anatolian barrier" (34), the mountain system separating the Egean zones of Anatolia from the central plains, which cut the arriving fishes off from the Egeopotamos [18].

Only one species of *Phoxinellus* is certainly living in Palestine, *P. kervillei* PELLEGRIN. The existence in Palestine of another species, *P. zeregi* HECKEL, has to be considered as doubtful (69). *P. kervillei* extends its distribution from Palestine through Lebanon and Syria to Central Anatolia. *P. zeregi,* claimed also for Palestine (25), was originally described by HECKEL (28) from Aleppo.

The genus *Phoxinellus* is found in Africa Minor, the Balkan Peninsula, Rhodos and part of the Near East. A brief consideration of some taxonomic points is indispensable for a discussion of the distribution problems of the genus.

Five species of the genus form a subgroup: they possess an incom-

[17] *V. capoeta* (GÜLDENST.), according to KOSSWIG possibly another member of his *V. damascinus* s. lat. (34).

[18] This mountain system has been claimed by KOSSWIG to form a barrier even for Tertiary migrants.

plete lateral line. BERG (11) created the genus *Pararhodeus* for them, but PELLEGRIN (52) and, later, TORTONESE (71) considered this char-

Fig. 10 — Distribution of subgenera of *Phoxinellus*. Triangles: *Phoxinellus s. st.* Black dots: *Pararhodeus*.

acter as demanding not more than a subgeneric separation. According to the latter arrangement *P. zeregi* belongs to *Phoxinellus s. str.* which has a complete lateral line, *P. kervillei* to *Pararhodeus*.

The position of *P. kervillei* must be treated in connection with other members of the genus. The localities recorded in the literature are:

P. (Pararhodeus) ghigii GIANFERRARI: Rhodos (23).
— — *libani* (LORTET): Lake Yammuneh (38, 49, 71).
— — *syriacus* (LORTET): East of Damascus; near Baalbek (38, 49); Barada (49); Shtorah (Lebanon), Ein Ktebe (SW-Syria: Jordan drainage system) (71).
— — *drusensis* PELLEGRIN: Mezraa (SW-Syria: Jordan drainage area) (52).
— — *kervillei* PELLEGRIN: Orontes (47, 49); Adana, Asia Minor (51); Lake Huleh (65, 71); Palestine (69); Central Anatolian lakes (34)[19].

In addition to these species TORTONESE described *P. rutiloides* from the Orontes River (71). We follow, however, TORTONESE's suggestion that the single specimen collected may represent only a subspecies of *P. kervillei* which is also reported from the Orontes. BERG (11) considered *P. syriacus* so similar to *P. libani* that he lists it as a subspecies of the latter. But TORTONESE (71) who had the opportunity to study numerous specimens of both species rejects BERG's contention. PELLEGRIN (52) mentioned the similarity of *P. drusensis* and *P. libani*. It is obvious that the systematics of *Phoxinellus (Para-*

[19] KOSSWIG does not mention a specific name of the *Pararhodeus* of Central Anatalia (l. c., p. 8/9), but he kindly informed the present writer that they probably belong to this species.

rhodeus) is by no means settled. Two species of the continental Near East have been found in single localities, *P. libani* and *drusensis.* But numerous specimens have been collected. *P. drusensis* lives in a locality which belongs to the drainage of the Jordan System. The same is true of *P. syriacus* which is, however, distributed over a wider area, located mostly outside the limits of the Jordan drainage. But all the three species *(libani, drusensis, syriacus)* are directly within or at the very margin of the distribution area of *P. kervillei.* This species has the widest distribution of all the *Pararhodeus* species. Its variability seems to be greater than ~~that~~ recognized by earlier authors (65). If now the Central-Anatolian *Pararhodeus* are also to be included in the species *kervillei* (see above) a revision of the species will very likely become urgent. As a result of the then probably broader concept of *kervillei* the status of the Syro-Lebanese species will have to be queried.

Taking the genus *Phoxinellus* as a whole its distribution follows a well known pattern: it is a disrupted perimediterranean one. Taking into account the taxonomic relationship of the genus with other Cyprinids it is probable that this genus originated in Europe but was pressed south by the glaciations. Several ways were open for the fishes proceeding from southern Europe to Africa and Asia. Continental bridges crossed the Mediterranean during the Pleistocene. The Italo-Sicilian and/or the Corso-Sardinian bridges to Africa may have played a role as certainly has the "Egeopotamos" with its extensive network of water ways. The Central-Anatolian lake system and adjoining rivers must have been deciding as mediators between the west of Anatolia and the east from where other water systems guided the fishes towards south and south-east. In the light of these considerations the systematic and the zoogeographic situation may mean that *P. kervillei* is oldest and still nearest to the stock of invaders into Asia Minor. Whether isolation in Anatolia resulted in differentiation remains to be seen. But in Lebanon and Syria speciation seems to have led to definite forms. It is interesting in this connection to review one of the characters which has consistently been used in the taxonomy of *Pararhodeus. P. ghigii* from Rhodos has 30 scales in the longitudinal line. *P. kervillei* has 37-42 scales (Palestine, Lebanon, Syria; no dates on record concerning Anatolian specimens). *P. syriacus* has 45-49, *libani* 48-55, *drusensis* 55-60 scales in the longitudinal line. A tendency toward increasing scale numbers, first exhibited by *P. kervillei,* may have become firmly established in progressing evolution. The three supposedly younger species are, with 45-60 scales, significantly smaller scaled than the older *P. kervillei.*

2. Cobitidae

In an earlier paper (69) it has been mentioned that the systematic status of the Palestinian species of *Nemachilus* is at present under study. There is, however, good reason to assume that the presence of

TABLE 4

Nemachilus: *Origin and Distribution*

Genus	Origin	Recent Distribution	Species recorded from Palestine
Nemachilus	S- and/or SE-Asia	Europe, Asia (palaearctic and oriental; Near East), East Africa	2—3

TABLE 5

Nemachilus: *Distribution Pattern of Palestinian Species*

Species	Distribution
insignis	Palestine, Lebanon, Jordan, Syria, Hatay (Asiatic Turkey); Persia*
galilaeus	Endemic
(*leontina*)	(Endemic)

* By way of accepting *N. persus* (HECKEL) as a synomym of *N. insignis* (HECKEL), fide TORTONESE (71).

N. insignis (HECKEL) and *N. galilaeus* (GÜNTHER) will not be questioned. Whether another species, new or not yet reported from Palestine, was also collected, is not yet decided. It is also to be asked whether *N. leontina* (LORTET) can be confirmed[20] (69). The countries of the Near East adjacent to Palestine harbour at least two more species, *N. panthera* (HECKEL) and *tigris* (HECKEL) (49, 71). *N. panthera* is particularly important, because it is reported from localities in the vicinity of Palestine both in the north and the east. Anatolia has a *Nemachilus* fauna of its own (34, 35). Since the species living there are also under investigation[21] and it is hoped that the relationship between the Palestinian-Syrian and the Anatolian species will become clarified by those studies now in progress, it is proposed not to enter into a more detailed discussion.

Briefly it may be stated that *Nemachilus* appears to be an oriental offspring of the earlier Cobitids in that region. *N. insignis* would be an old species since it exists in the far-away Persia (at least an almost indiscernible form exists there (71). The genus is also known from Africa where *N. abyssinicus* BOULENGER was discovered[22]. This

[20] The original description is still the only record of this species. It is unknown whether specimens are being kept in collections.

[21] Results published in part (72).

[22] As far as our information goes, not more than one specimen has been secured (Lake Tsana) (18).

is a very limited success of a genus that reached the African continent from the Oriental Region.

3. Clariidae

The following outline survey of the Siluroid fishes common to the Oriental and the Ethiopian Region will provide the base for the discussion of the evolutionary history of *Clarias lazera*.

We draw with advantage on the fundamental studies of REGAN (56, 57) who based his conclusions on the comparative anatomy as well as on the geographic distribution of the catfishes ; further on the work of BOULENGER (17, 18) and that of DAVID (20) who subjected the *Clariidae* to a thorough examination of their body structure in general and of the skeleton in particular.

The Siluroid families common to the Oriental and the Ethiopic Region are the *Schilbeidae*, the *Bagridae*, and the *Clariidae* (fig. 11). While the first two of these families include no genera common to the two regions, indicating that the Asiatic and the African sections of them must have been separated early, there occur two identical genera of the *Clariidae* in South-East Asia and in Africa. Furthermore, REGAN concluded from a study of the anatomy that the *Clariidae* are derived from the *Bagridae* and, therefore, younger than these.

The *Bagridae* gave rise to still more families (see fig. 12). Africa has the endemic *Amphiliidae, Synodontidae, Malapteruridae*. Asia has the endemic *Pangasiidae, Sisoridae, Amblycepidae*, etc. All of these show in their body structure indications of their descendance from the *Bagridae*. But since every one is restricted either to Africa or to Asia there is no question as to the region of their origin. The *Clariidae*, however, pose definitely a problem since they developed at a time when the Oriental and the Ethiopian Region were separated by the Tethys Sea. Yet, the Clariid genera *Clarias* and *Heterobranchus* occur in Africa as well as in Asia (fig. 11).

The recent *Clariidae* are represented in Africa by seven genera, in South-East Asia by three. As mentioned above two Clariid genera are common to the Oriental and the Ethiopion Region, *Heterobranchus* and *Clarias*, while Asia has one endemic genus and Africa five. It is noteworthy that the Asiatic *Saccobranchus*, assigned to the *Clariidae* by REGAN (56), is said by DAVID to be close to *Clarias* but to have broken away from the main stem of the *Clariidae* before the other genera evolved. On the other side the endemic African genera of the *Clariidae*, except *Dinotopterus* [23], seem to be derived from *Allabenchelys* or from a possibly extinct form near to the latter.

Allabenchelys is considered by DAVID as one of three subgenera of *Clarias* s. l., the other two being *Heterobranchoides* and *Clarias s. str. Clarias* and *Heterobranchoides* are living in Africa and South-East Asia, *Allabenchelys* only in Africa. On the whole the Clariids have a much larger species representation in Africa (45-50 species) than in Asia (about 5 species).

In spite of the smaller recent representation of the *Clariidae* in Asia their geographic origin is most likely Asiatic. Several circumstances are in favour of this view. The earliest branch of the primitive Clariid stem, *Saccobranchus*, is represented only in India. The earliest fossil record recognized as Clariid [24] is from the Siwalik deposits. It was described by LYDDEKKER, in 1886, as *Clarias falconeri* and *Heterobranchus palaeindicus* (53), but DAVID reassigns the latter to *Clàrias* (*Clarias*). Both are dated as Lower Pliocene. But the early splitting-off of *Saccobranchus* compels us to ascribe an even higher age to the old stock of the *Clariidae* (see above, and DAVID, l. c.).

[23] Misspelled in fig. 11.

[24] Fragments from Egypt tentatively ascribed to *Clariidae* and dated as Eocene and Lower Oligocene, respectively, by PEYER (l. c.), were too fragmentary and too uncertain as to the period to be accepted.

ASIA	AFRICA
SCHILBEIDAE	SCHILBEIDAE
BAGRIDAE	BAGRIDAE
SILURIDAE	
AMBLYCEPIDAE	
SISORIDAE	
CHACIDAE	
PANGASIIDAE	
	AMPHILIIDAE
	SYNODONTIDAE (=MOCHOCIDAE)
	MALAPTERURIDAE
CLARIIDAE	CLARIIDAE
SACCOBRANCHUS	
CLARIAS	CLARIAS
Clarias	Clarias
Heterobranchoides	Heterobranchoides
	Allabenchelys
HETEROBRANCHUS	HETEROBRANCHUS
	CLARIALLABES
	GYMNALLABES
	CHANNALLABES
	DINOPTERUS
	UETIGLANIS

Fig. 11 — Recent representation of Siluroid fishes in Asia and Africa. Systematic subdivision of families broken down to subgeneric level. Families, genera and subgenera indicated by different print type. Based on sources quoted in the text.

The earliest (and only) Tertiary record of African Clariids [24] is the finding of fish remnants in the Natron Valley of Egypt, dated as Middle Pliocene and named *Clarias* by PEYER (53). DAVID ascribes them to *Clarias* (*Heterobranchoides*), but admits that they may belong to the genus *Heterobranchus* since the differential character of the latter genus, the adipose dorsal fin, was naturally not preserved in the fossil. Fossil deposits older than Middle Pliocene do not contain any remnants of Clariids (20). The

coordination of the datas and localities of the fossil *Clariidae* just mentioned presented the main reason for favouring the Asiatic origin of the family. But it is felt that the view that *Saccabranchus*, an endemic Asiatic genus, is the earliest offshot of the *Clariidae* contributes equally toward this assumption.

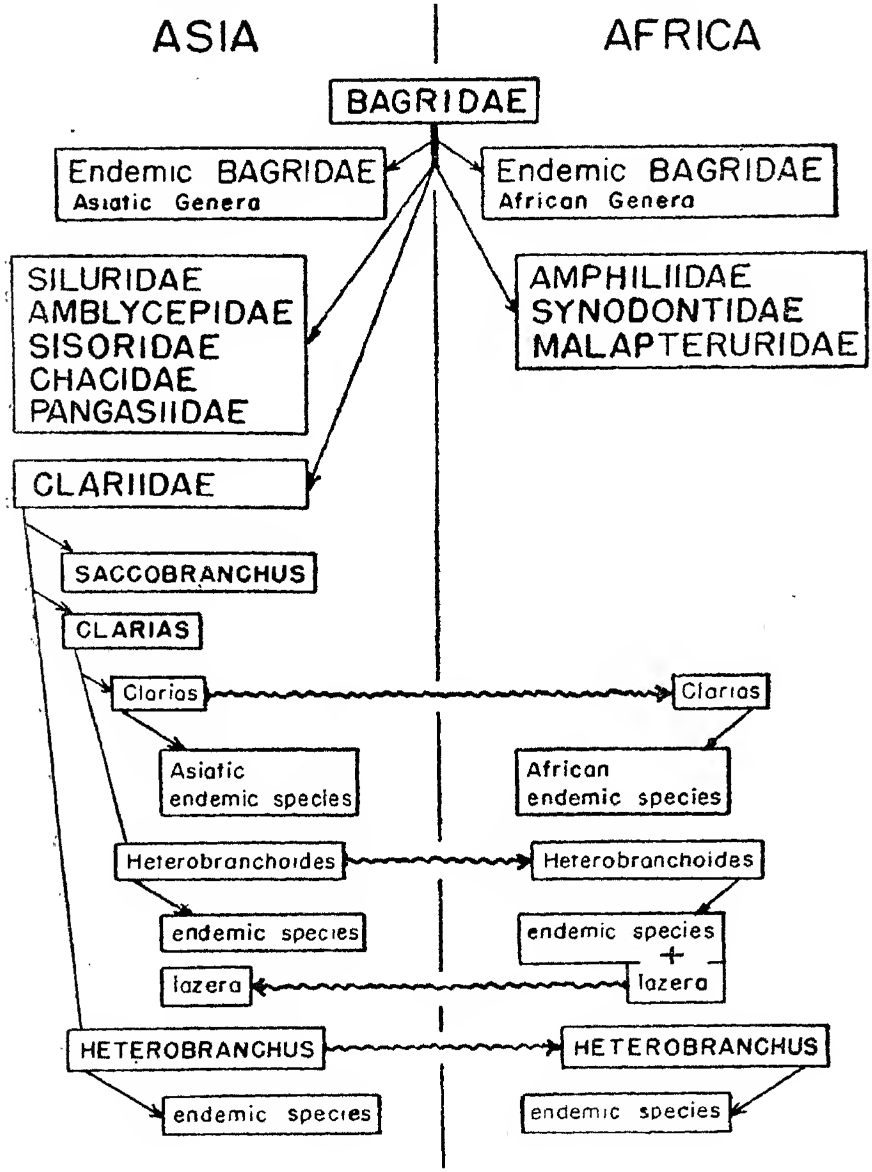

Fig. 12 — Diagrammatic representation of the hypothetic relations, phylogenetic and geographic, of some of the Asiatic and African Siluroid fishes (based on the sources quoted in the text). Several endemic Clariid genera of Africa are ignored. Straight lines with arrows indicate descendence; wavy horizontal lines with arrows indicate intercontinental migrations.

Clarias (Heterobranchoides) lazera C. V. is the only species of the family found in Palestine. It has a wide distribution in tropical and East Africa. With *C. (Heterobranchoides) mossambicus, gariepinus, capensis,* and *senegalensis* it forms a special group within the subgenus. In the Near East where it is by no means restricted to Palestine it is recognized as the only species although some authors, not taking note of BOULENGER's work (17, 18), still carry the names of *C. orontis* GÜNTHER and *C. syriacus* C. V. *C. orontis* was originally described from the River Orontes (25), but was also found as far north as Lake Antiochia (35). *C. syriacus* was first described from Syria with no specific locality given (19). The Asiatic area occupied by *C. lazera* seems, therefore, to be a rather narrow belt extending along the east coast of the Mediterranean north to the point where the South Anatolian mountains approach the sea. This situation is very characteristic and will be commented on below.

All the facts concerning the systematic relations and the geographic distribution of *C. lazera* point to the conclusion that it evolved in Africa as an offshot of the old *Heterobranchoides* which entered Africa together with other Asiatic fishes. *Clarias s. str.*, another subgenus of the same genus (fig. 12), was also among the invaders. So was *Heterobranchus*, another genus of the same family. No relict of these three fishes survived to recent times in the Asiatic Near East which had been traversed by the migrators. No fossil remnant of them has been discovered there. We prefer not to speculate on the possible causes of their disappearance from that area. However, when *C. lazera* had eventually developed in Africa, it joined the migratory movement starting from Africa toward Asia. *C. lazera* and the Palestino-Syrian *Cichlidae* are the only survivors of that invasion in the Asiatic Near East.

The problem of dating the African-Asiatic fish migration requires more data than are available at present. As will be seen later we are in a slightly better position with regard to the *Cichlidae* than with regard to *C. lazera*. It must be kept in mind that the arrival of this African fish in the Near East must have occurred subsequent to the arrival of the Asiatic *Heterobranchoides* in Africa. A certain length of time must be allowed for the evolution of *C. lazera* in Africa. This time at least elapsed between the two migrations. We have already pointed out that increasing aridity increased the risks of the migration through the South-West Asiatic region for the fishes taking the route towards Africa. Desiccation became stronger for a considerable time; chances of succeeding under such adverse conditions in the zone adjacent to North-East Africa became slim. South-East Asiatic fishes had spread extensively in the Near East. We have seen in earlier sections of this paper that wide stretches of Anatolia had been colonized by a number of fishes of that group. *C. lazera* is an extraordinarily hardy fish. It is used to fairly high salt contents of the water in which it lives; it survives inspite of very poor oxygen contents of the water on

account of accessory gills adapted to air breathing. This also enables the fish to live for prolonged periods outside the water; as long as a certain amount of moisture is guaranteed on the land, it moves energetically and makes rather good headway. One should therefore think that this fish is capable of making use of conditions intolerable for many other species. If with all its adaptations *C. lazera* did not spread beyond the narrow land strip it actually occupies we may conclude that outside this area conditions were already too steppe- and desertlike when the fish arrived. This may also have compelled it to stop its progress towards Anatolia. But an alternative, or complementary, factor must be mentioned. *C. lazera* is formost a tropical fish. We have no data indicating to what extent the species can tolerate decreasing water temperatures. Seasonal migrations toward warm springs, culminating in spawning, have long been reported from Palestine (38, 76). Nevertheless, spawning has actually not been observed as yet. However the eggs and the hatched larvae of *C. lazera* have recently been found in considerable numbers in warm springs on the shore of Lake Tiberias[25]. If eggs and larval stages of the species should ultimately prove to be dependent on high temperatures for their development, a factor limiting the northern range of *C. lazera* would be established.

The main points of the history of *C. lazera* and its ascendants may now be summarized. The *Clariidae* are descendants of the Asiatic *Bagridae*. Of the products of differentiation of the *Clariidae* in their homeland, two genera, *Heterobranchus* and *Clarias*, eventually reached Africa during the late Tertiary. No remnants of this migration exist in the Asiatic Near East. But in Africa the species *C. lazera* evolved. Today it is widespread in that continent and inhabits also a narrow zone in the Asiatic Near East. The latter was colonized by the species late in the Tertiary when migration waves brought more freshwater fishes from Africa to Asia. No definite time can be allotted to the migration of *C. lazera*. Ecological considerations, though useful in giving direction to the discussuion, will have to be supplemented by many data from various other fields. We are still far from a full understanding of the present distribution of *C. lazera* and its history.

4. Cichlidae.

Three Cichlid genera are found in Palestine: *Tilapia*, *Tristramella* and *Haplochromis* (Table 6). Taxonomic questions have been treated in previous publications (10, 69) and will therefore be commented on in passing only.

The zoogeographic situation is characterized by the following facts. All the three species of *Tilapia* are essentially African species. *Tristramella* is an endemic genus occuring in the Jordan and Damascus depressions. The representative species of *Haplochromis* is endemic within the drainage of the Jordan System, while the genus itself is mainly

[25] Unpublished observations.

TABLE 6

Cichlidae: *Origin and Distribution of Palestinian Genera*

Genus	Origin	Recent Distribution	Species recorded from Palestine
Tilapia	Africa	Most of continental Africa; Palestine; SW-Syria	3
Haplochromis	Africa	Tropical and North Africa; Palestine; SW-Syria	1
Tristramella	Syro-Palestine (Jordan-Damascus Depression)	Palestine; Syria	2

African. This is sufficient to show that an immigration of African Cichlids has taken place. But it is also seen that from the various immigrants new forms have derived in the Near East.

The only finding of fossil *Cichlidae* in our region (Galilee, Israel) was dated as Upper Pliocene (5). Remnants of two species were discovered, but no category lower than the family could be determined.

Tristramella sacra (GÜNTHER) is confined to the Jordan Valley in Palestine. *Tristramella simonis* (GÜNTHER) has three subspecies. Of them *T. simonis simonis* (GÜNTHER) and *T. simonis intermedia* BEN-TUVIA and STEINITZ are also found in the Jordan Valley only. But it is important to keep in mind that a third subspecies, *T. simonis magdalenae* (LORTET) lives in the vicinity of Damascus. Since the Damascus Depression is definitely separated from the Jordan Depression since

TABLE 7

Cichlidae: *Distribution Pattern of Palestinian Species*

Genus	Species	Distribution
Tilapia	*nilotica*	Tropical and North Africa; Palestine
	galilaea	Tropical and North Africa; Palestine
	zillii	Tropical and North Africa; Palestine
Tristramella	*sacra*	Lake Tiberias (Jordan Valley)
	simonis	Jordan System; vicinity of Damascus

the Upper Pliocene at least (54), the species *T. simonis* is at least of that age. It must have lived before that period in the uniform Jordan-Damascus Depression. From the isolated northern population the subspecies *magdalenae* evolved. The early *T. simonis* probably developed in the Jordan-Damascus depression from a primitive *Tristramella* which was also the parent of *T. sacra*.

The presence of *Cichlidae* in Palestine during the Upper Pliocene is substantiated by the fossil remnants referred to above. But these are inconclusive with regard to *Tristramella*. As to the latter's ascendence the question is whether *Tilapia* can be claimed as parent form. Those structural characters of the various species of *Tristramella* that have been studied extensively in order to ascertain the systematic position of these species (57, 75), give evidence of a clear-cut difference between the genera *Tilapia* and *Tristramella*. But no particular study has been made of the two genera in order to establish whether structural characters suggest a derivation of the genus *Tristramella* from that of *Tilapia*. This would imply a fairly early immigration of *Tilapia* from Africa, early enough to account for the evolution of the *Tristramella simonis* stock which spread throughout the Jordan-Damascus Depression.

Tilapia has probably entered the Near East in considerable strength. *T. galilaea* (ARTEDI), *T. nilotica* (L.) and *T. zillii* (GERVAIS) are the only survivors. All of them have adapted themselves in Africa and Asia to a broad variety of conditions. They inhabit a vast area. It is significant that among only three species of *Tilapia* established in French North Africa in a semiarid region very similar to Palestine, *T. galilaea* and *T. zillii* have been found (48) [26]. The identity of species in African and in distant Palestinian waters suggests a relatively late immigration. For how long migration from Africa could continue under deteriorating Pliocene conditions, or even later than Pliocene, is a question to be put first to geology and paleoclimatology. But late immigration is also suggested by the geographic limits of the three species. In discussing the distribution of *Clarias lazera* we pointed to the connection between climatic condition and the dispersal within a narrow belt of relatively rich water resources in the late Tertiary. *Clarias lazera* is found reaching northward to the Syro-Anatolian border region. It was also mentioned that *C. lazera* is a species which can survive under conditions absolutely prohibitive to the survival of the majority of freshwater fishes. The species of *Tilapia* quoted here are far from being capable of enduring conditions tolerable to *Clarias lazera*. Under the conditions prevailing in the late Tertiary the *Tilapiae* could not be expected to extend their range as much as *Clarias*. But within the overlapping part of their distribution areas all three species of *Tilapia* are found in the same water bodies as *Clarias*.

26 It is not less significant that among the two Siluroid fishes of the same re-

TABLE 8

Subspecies of Palestinian Cichlidae

Species	Subspecies	Recent Distribution
Tilapia nilotica	1. *ssp. typica*	Palestine: coastal rivers and Jordan System (Ein Feshkha excepted)
	2. *exul*	Ein Feshkha
Tristramella simonis	1. *simonis*	Lake Tiberias (? + Lower Jordan System)
	2. *intermedia*	Lake Huleh (occasionally in Lake Tiberias)
	3. *magdalenae*	Vicinity of Damascus

Speciation manifestly occurring in one of the *Tilapiae* was discovered in an isolated population living under peculiar circumstances of thermal and salty springs (63, 64). *T. nilotica exul* STEINITZ was found in Ein Feshkha, one of numerous warm springs scattered around the Dead Sea. The springs are remnants of Pleistocene volcanism. The accumulation of salts in the Dead Sea which made its water unsuitable for higher organisms took also place during the Pleistocene. *T. nilotica* still living in the Jordan down to the ecological barrier of Dead-Sea conditions, inhabited the fresh waters of the earlier lake that filled the Dead Sea Depression. The fishes entered the warm springs of Ein Feshkha draining into the freshwater lake. Trapped by the increasing salt contents of the lake they became confined to a very small area. Isolation under so special conditions must have favoured the evolution of a subspecies whose age is according to the geological evidence determined as Pleistocene. A peculiar form of an *Aphanius (Cyprinodontidae)*, preliminarily named *A. aff. dispar, Ein Feshkha* (69), lives side by side with *T. nilotica exul* and has probably arisen in a comparable fashion as will be reported later.

Haplochromis flavii-josephi (LORTET) has its nearest relative in North Africa. The genus is foremost tropical. *H. desfontainesii* (LAC.) of North Africa is so similar to the Palestinian species that sometimes the latter was considered synonymous with the former. Both species exhibit an interesting similarity in adaptation to certain conditions. *H. desfontainesii* seems to favour in the semi-arid regions of North Africa warm spring water (18, 48). *H. flavii-josephi*, living in semi-arid Palestine, is also only found in places where clear, warm water is abundant. Springs and their proximity are clearly preferred. It must be left to a detailed comparative study of the two species to decide whether ... be recognized as descendants of a common parent.

The particular distribution of *H. flavii-josephi* in Palestine gives no clue as to the time at which the early *Haplochromis* may have arrived from Africa, but raises problems hitherto unsolved. The coastal rivers of Palestine are not inhabited by *H. flavii-josephi*. In the Jordan System it has been found from the entrance of the river into Lake Tiberias to the south end of the Jordan and in all the tributaries investigated[27]. Lake Huleh and the Upper Jordan System are apparently not inhabited by it. We do not know what the reason of this restriction may be. It is the same geographic limitation to which *Tristramella sacra* is subjected. The latter species has also not been observed in Lake Huleh[28] and the Upper Jordan System. Lake Huleh and Lake Tiberias which formed for a long time one basin are separated at least since the beginning of the Pleistocene as has been mentioned above. It is hardly believable that *Haplochromis* should not have been in the Jordan Valley before that date. As to *Tristramella* its presence in the Damascus region is evidence that it inhabited the Jordan Valley prior to its dissection into the northern uplifted portion including Lake Huleh, and the southern portion, south of the latter. *Haplochromis* may have become extinct from the northern Jordan Valley following its separation from Lake Tiberias. This could be assumed for *Tristramella sacra* or its forerunner, too. *Tristramella sacra* became even more restricted than *H. flavii-josephi*. It has not been observed outside Lake Tiberias. Ecological factors not yet investigated are probably responsible for this limited distribution (compare part III, 3).

The problem of dating the immigration of African Cichlids has already been touched several times in this paper. The facts known so far do not point to a precise date; they rather outline rough limits which we shall try to narrow down as much as possible. Even fossil remnants, bound to give critical evidence in many cases, are of no primary value because of their taxonomic insufficiency. We have to approach the problem from yet another angle. Emigration from Africa in the direction of Asia during the Middle and Upper Miocene could take advantage of the broad continental bridge binding Arabia to Africa. The Suez Graben, at first a semi-marine basin, later more and more of continental character, would probably not have been a serious obstacle for certain Cichlids. But such an early advent of Cichlids in Palestine is not only not supported by paleontological evidence, it is not at all warranted by the present situation. In the Lower Pliocene the land connection between Africa and Asia became so narrow (fig. 3 b) that chances for migration were certainly slim. The Upper Pliocene was more favourable to migration on account of the broadened contact of the two continents (fig. 4).

27 A Transjordanian locality was reported by PELLEGRIN (52) and TORTONESE (71): Mzerib, in the drainage zone of the Jordan System.

28 The contradicting report of LIEBMAN would be the only one of its kind; it is probably due to a misidentification (37).

In the Plio-Pleistocene Transition period the Isthmus of Suez became established diminishing again chances of fish migration. In the meantime the aridity of the Near East increased and although several pluvials occurred during the Pleistocene, paleoclimatologic data are not sufficiently definite to establish at what time fish migration must have come to a standstill. Orographic conditions were also changing extensively involving the course of waters and closing routes that had been used by migrating fish.

Summarizing we find that paleogeographic features seem to be in favour of the emigration of Cichlids from Africa during the later part of the Miocene, but that nothing of zoological information would support such an assumption. While paleogeographic factors are not particularly favourable to a Lower Pliocene migration it can not be excluded from a zoological standpoint. The latter date is also closer to that of the Upper Pliocene on which most indications converge: the few fossils savailable are of Upper Pliocene age; the species identity of *Tristramella simonis* in the Jordan and the Damascus region requires the presence of the species in the Near East before the close of the Pliocene; the endemic character of the genus *Tristramella* moves the time limit of the immigration of its parent even more back into the past; the present distribution of the Cichlids in the Near East disfavours an early immigration; species identity of *Tilapiae* in Africa and Palestine suggests late immigration. However, it is a question whether and for how long migration could go on during the Pleistocene. If, thus, the Upper Pliocene is most probably a time of Cichlid immigration it need not be so to the exclusion of a longer poriod. We have already said that the *Tilapia* invasion has probably been considerable in number of species; we should now add that the Cichlids as a group must have immigrated in considerable strength. But we should also emphasize that their invasion was probably in progress over a longer period. Taking taxonomic categories as a measuring rod we tentatively give the parental stock of *Tristramella* the first place in the time order, to *Tilapia nilotica, galilaea* and *zillii* the last; accordingly the forerunner of *Haplochromis flavii-josephi* may claim an intermediate place.

This section of our study can not be concluded without a brief mention of the question whether the invasion of the Cichlids could have been made wholly or in part by way of the sea. The Cichlids are secondary fresh water fishes (MYERS, 42). Some features of their particular geographic distribution in the world can not be explained unless the sea, or at least the shallow coastal waters, are resorted to as a pathway. Numerous Cichlids, amongst them species of *Tilapia*, are known as highly euryhaline, others have been shown to survive for a long time in pure sea water (43). All the three species of *Tilapia* recorded from Palestine have been observed in various localities of more or less marine character and in the lakes connected with the Suez Canal (18, 46). However in Palestine the same species have never been observed to

approach even the estuaries of the coastal rivers in which they live. This is, of course, no proof that a marine invasion of Cichlids is to be excluded. But as experimental data contributing to this problem are not available we see no point in further speculation.

5. Cyprinodontidae

The geographic distribution and evolution of the *Cyprinodontidae* of the Mediterranean Region was dealt with in a previous paper in 1951 (66). In a later paper (69) an acccount was given of the taxonomic status of Palestine's *Cyprinodontidae*. It was hoped that the problems of the systematics of that small number of fishes would in the meantime become clarified and, thus, light be thrown on some obscure points of their history. This hope did however not materialize. Only very little has otherwise been published since, relevant to our subject.

Aphanius fasciatus (VAL.) has been found in coastal rivers and swamps of Palestine. It is a species known from all but the westernmost Mediterranean coasts (66). Living in the sea it enters freely rivers; it seems to thrive equally well in freshwater. Reproduction occurs in fairly concentrated sea water (68); it has not been reported whether it takes place also in fresh water. *A. fasciatus* has not been observed in landlocked waterbodies [29].

A. sophiae (HECKEL) - *cypris* (HECKEL) is found in Palestine in waters of the coastal plain and in the Jordan System. An isolated population is known to exist in Ein Feshkha (64), a spring pool on the north-west shore of the Dead Sea. It is probable that more isolated populations exist in the springs and rivers joining the Dead Sea from the east. In view of the speciation shown to be taking place in other fishes of Ein Feshkha (see *Tilapia nilotica exul*, earlier in this paper, and *A. dispar*, below) the isolated *A. sophiae-cypris* population should be analyzed again. However, as has been reported repeatedly (66, 69) the systematic status of the whole species ranging from Anatolia through Syria, Lebanon, Palestine, Trans-Jordan, and probably Iraq and Persia, is by no means cleared up.

Wherever the species is reported from, it is obvious that inspite of its tolerance of a certain degree of salinity it is never met in the sea or the litoral zone.

As has been reported lately (69), *A. dispar* (RÜPPELL) does not occur in any continental water body in Palestine. All records of the pres-

[29] BODENHEIMER's report (51, p. 424) from Beth Shean, a locality belonging to the Jordan drainage area, is probably founded on an error. But recently SMITH (61) published a note ascribing to this species two specimens found in a highly concentrated salty and sulphurous thermal water in Cyrenaica. This record is of great interest. It not only raises the question whether the population living there differs in its taxonomic make-up from the free-living *A. fasciatus*; it also can not fail to throw light on the problem of crossbreeding of this species with *A. dispar* (NORMAN, TORTONESE) which is said to live side by side with *A. fasciatus* (61).

ence of this species in such places are either probably or definitely referable to forms significantly distinct from *A. dispar*. All but one continental locality[30] listed for the so-called *A. dispar* are situated in the Dead Sea Valley. Some of these localities have changed so rapidly and so thoroughly since the Cyprinodonts were recorded that no fishes are living in them today. Of some of the isolated populations no collection is on record. At present, specimens of three different populations are under investigation. It has been reported (69) that one group has to be designated as *A. richardsoni* (BOULENGER), while the others have been named preliminarily according to their respective localities (*A. aff. dispar: Ein Feshkha* and *A. aff. dispar: South Usdum: S'dom).* There is no doubt that all these forms are relatives of *A. dispar* (RÜPPELL). Details of their interrelations are the subject of the study mentioned above. Among the differential characters of the three forms are fin-ray counts and scaledness. The biotopes in which the fishes are living are different in temperature and salinity (total and composition). It is interesting to note that the temperature influences in certain fishes the number of vertebrae and fin rays phenotypically (22, 70). None of the authors working on these problems has, to our knowledge, observed a significant influence of the temperature on number, relative size, and imbrication of scales. On the other hand it has been shown in a detailed analysis by AKŞIRAY (1) that scale features of the kind mentioned are of a genotypic character in certain Cyprinodonts and appear in various combinations in different populations of the same or of very closely related «species». The differentiation of those different forms is supposed to have taken place during and since the Pleistocene, when isolated populations were created. A genetic hypothesis was tentatively put forward to account for the various types of scale patterns found among Anatolian Cyprinodonts (1).

It has been explained in the section of this paper dealing with the *Cichlidae* that the isolation of fish populations living now in the rivers and springs along the shore of the Dead Sea is to be dated as Pleistocene. *A. dispar* was previously (66) considered to be of Tethys age. This age determination was linked with the assumption that the various Dead Sea populations discussed here belong to *A. dispar*. A reconsideration of the question will perhaps be required when the systematic position of the populations is fully worked out. *A. richardsoni* may not be an offspring from *dipsar*; both may be descendants of an older parent stock which gave also possibly rise to *A. fasciatus*. *A. dispar* is found today in the litoral waters of the Red Sea and of part of the Indian Ocean (66). It also entered the Mediterranean Sea via the Suez Canal (40). Recently SMITH (61) reported the presence of *A. dispar* in a land-locked spring pond in Cyrenaica; one specimen only was collected. But in view of what has been said of the Palestinian *Aphanius* forms of the Dead Sea Valley and of the absence from Palestine of

[30] Lake Tiberias was listed by ANNANDALE (2), but is questioned (69).

land-locked true *A. dispar*, confirmation of the diagnosis is imperative before conclusions can be drawn from the new record.

KOSSWIG (30) advanced the opinion that the circum-mediterranean and the Near East Cyprinodont fishes are best understood as Tethys relicts. This hypothesis has proven very fruitful. It has been proposed (66) that at least two main stocks of *Aphanius* existed in the mediterranean Tethys, the one from which *A. dispar, fasciatus, iberus* and the Dead-Sea Valley forms evolved, and the other that gave rise to *A. cypris-sophiae* and, probably, to other endemic Anatolian forms. The slow rise of continental blocks formerly covered by the Tethys was an excellent opportunity for litoral fishes to invade lowlands which later became strongly elevated. In this way whole populations were land-locked. The distribution of *cypris-sophiae* taken as a systematic entity, over a vast area of the Near and Middle East is proof of its relatively high age. It remains to be studied whether populations of distinct taxonomic character developed in consequence of the geographic split-up.

The distribution of the *dispar* relatives over places along the Dead-Sea shore finds a convenient explanation if the freshwater lake that occupied the deepest part of the depression, is accepted as the past medium of communication which harboured the common ancestors of the isolated populations. It is implied that these ancestors also inhabited the Jordan System. Why, then, did they disappear from the river and its tributaries? There is no answer to that question. Attention should be given to another faint possibility hinted at by geological research. We mentioned that a marine and semi- marine invasion toward the Dead-Sea Valley might have occurred via the Beersheba Gulf etc. during the Lower Pliocene (54), but that the geological findings are not conclusive. A solution of that kind would be better compatible with the apparent intolarence of pure freshwater of those fishes [31].

6. Blenniidae

Freshwater blennies exist in almost all Mediterranean countries. Since they belong to a marine family they have to be classified as secondary freshwater fishes. Although well known from numerous European localities since the early 19th century their systematic status has not been worked out satisfactorily. Descriptions were frequently not sufficient to recognize the various species created by the authors. It so happened that several localities seemed to be inhabited by more than one species of freshwater blennies. This situation as well as the creation of more than one species for the freshwater blennies in general, was not considered to be a true representation of the evolutionary events and processes which led to the derivation of these freshwater fishes in the whole of the perimediterranean countries. Consequently, it was proposed that only one species

[31] Dr. H. MENDELSSOHN has kindly informed me that the fishes of the Ein-Feshkha population (the only ones studied in this respect) do not stand well freshwater when kept in the laboratory; but they thrive when given half-strength seawater.

existed in the whole area. Two attempts were made to account for the evolution of a uniform *Blennius*. ROULE (58) suggested that *B. pavo* RISSO be the marine parent species which immigrated at many places upstream and, under freshwater conditions, became transformed to *B. fluviatilis*; in other words he proposes the polytopic evolution of a new species. DE BEAUFORT (8) recently suggested that *B. fluviatilis* be a euryhaline species living in the sea, but freely entering freshwater at different places. ERAZI (21) joined ROULE in applying his views to Turkish freshwater blennies. The implications of the hypothesis advanced by ROULE were treated by the present author in a preceding paper (62). There, it was shown that neither the comparative-anatomical basis of his assumption was appreciated by ROULE himself, nor had an attempt been made by that author to supply ecological data in support of his opinion. DE BEAUFORT's hypothesis, on the other side, is not borne out by facts, as the freshwater blennies have nowhere been found in the sea.

It should be clear that the problem of the evolution of the freshwater blennies can to a certain degree be separated from that of the systematic status of the populations actually found in freshwater in different localities. With regard to this point the primary task would be making sure whether one locality is inhabited by one or more taxonomic units; then, comparison of populations from different localities should definitely clear the question, how many species should be recognized among the perimediterranean freshwater blennies.

Studies of recent years have brought some progress concerning the last two questions. The blennies of Lake Tiberias were found to belong to one species (62; 69) contrary to what had been thought previously. A clarification of that point was conveniently based on a study of many specimens. The situation is less satisfactory with regard to the blennies of coastal rivers in Palestine. There, *Blennius* seems to be rare; only one specimen was collected. Although a first examination (69) showed that it is different from the species found in Lake Tiberias no final conclusions could be drawn. On the other hand freshwater blennies from two different Anatolian localities appear to differ not only from each other but also from the Lake Tiberias form.

It is a question of secondary importance which of the published species names, if any, should be applied to those different forms. The *Blennius* of Lake Tiberias was named *B. vulgaris* in the preceding publications mentioned (62; 69). Whether this was justified must lastly be judged by comparing those specimens with the type. The coast-river blenny has not yet been named (69).

Tunis, Libya and Egypt are the only Mediterranean countries from which freshwater blennies are not reported. In the west-, north- and east-sections of the perimediterranean belt their occurrence is more or less continuous. To explain the evolution and distribution of the numerous separate populations no single, rigid, theory is called for. Marine relict and active immigrant are no alternative propositions. It is hardly

believable that geological evidence will point to just one event in the perimediterranean zone apt to explain the history of freshwater blennies in the entire region. In the geological history of Palestine we found one event which may provide an explanation of the land-locked blennies of Lake Tiberias (54; 62). A Lower Pliocene ingression of the Mediterranean is known to have extended into the Tiberias basin. If a marine *Blennius* came up with that ingression it survived in Lake Tiberias and its tributaries only, but must have died out in Lake Huleh which was part of the greater Pliocene East Galilean Basin. In any case we would consider the Tiberias blenny as a marine relict. Active immigration into a river milieu was probably the first step of the transformation into those freshwater blennies found in the coastal rivers of Palestine, Lebanon, etc.

III. GENERAL CONSIDERATIONS.

1. Asiatic-African fishes, absent from Palestine.

Mention has been made earlier in this paper of the scarcity of paleontological evidence. The actual record of Pliocene *Cichlidae* (5) has been cited in the respective paragraph. The finding of hitherto undetermined fishes from Jebel Usdum (54) has been reported in the section of this paper dealing with the paleogeography, although the freshwater origin of these fishes is not established. That much more of fossil material must be hidden in the rocks of Palestine is a plain consequence of the studies presented here. But fossil remnants are not only to be expected of the ascendants of the fishes living in Palestine at present. Zoogeographic data from other countries of the Near East point directly to the occurrence of fishes in Tertiary times in Palestine that have since entirely disappeared from this country.

The *Cyprinidae* of the Oriental Region have probably sent out a large variety of species toward the west of which *Barbus, Tylognathus* and *Garra* are the survivors in Palestine. Another genus, *Barynotus*, today represented in the Near East by *B. albus* (HECKEL) and *B. luteus* (HECKEL) from Lebanon and Syria (28), and *B. verhoeffi* BATTALGIL (6) from Lake Amik might well have had a broader distribution in earlier times, entering also Palestine, although it is not known from Africa[32]. *Barynotus* is a small genus with its main area in South-East Asia. — *Barilius* is a different zoogeographic type. Its home is in the Oriental Region where about 20 species are known, mostly from India; in Africa it has about the same number of species. Although the genus has been far from being as successful in Africa as *Barbus*, it still gave rise there to three new genera (*Engraulicypris, Leptocypris, Cheloethiops*. 18; 45) with 9 species. If we take the view that *Bari-*

[32] GÜNTHERS's *Barynotus lagensis* (25) is to be placed with *Barbus*, see BOULENGER (18) and WEBER—DE BEAUFORT (79).

lius has, on the whole, declined since the Tertiary in both its Oriental and African area, it is no wonder that only one species has survived the hardships of the geophysical changes in the Near East. *B. mesopotamicus* BERG is known from Central Iraq. Its allies live in India. From all the African species it differs more than from his Oriental relatives (12). We have, of course, no means to prove that *B. mesopotamicus* is the last member of a continuous population of *Barilius* in loco. Episodes of emigration from, and remigration to, the Iraq basin could well have played a role in the history of Near East fishes. In any event, the presence of a *Barilius* in the Near East is evidence of the migration of Asiatic fishes which so profoundly changed the character of the African fish fauna. Among its recent elements we find two more Oriental genera of the *Cyprinidae* with no living representatives in the Middle and Near East, *Labeo* and *Rasbora*. *Labeo* has more than 50 species in Africa, *Rasbora* is represented by one species only.

It is not intended to give a synoptic picture of the *Cyprinidae* common to Asia and Africa. The facts reported here suffice to indicate how varied the fate of the genera involved is. The size of the present distribution area here and there, the number of recent species at both ends of the route, the new genera evolved since the migration, populations in the intermediate area: these and many more points would corroborate the belief that inspite of many mishaps adaptability has been instrumental for the *Cyprinidae* to become one of the most successful fish families.

A few remarks regarding three other families also represented among the Tertiary migrants from Asia to Africa will add strength to the opinion just stated. The *Ophiocephalidae*, the *Anabantidae* and the *Mastacembelidae* are old Asiatic families; distribution and diversity of genera support that stand. It is generally accepted that their representation in Africa by oriental genera is evidence of a late (post-Tethys) immigration. *Ophiocephalus* has about three African species, *Anabas* about 15, *Mastacembelus* about 35. An enormous life tenacity distinguishes the fishes of these families; they live in fresh and brackish water, are tolerant of low oxygen concentrations in the water, even survive and migrate — some for several days — on land. These physiological adaptations are equalled by marked morphological specializations among which devices for breathing in the air are prominent; the specialization of the *Ophiocephalidae* and the *Anabantidae* exceeds that of the *Mastacembelidae*. But a certain ecological rigidity is often the counterpart of specialization. That may be one of the causes of the complete extinction of the *Ophiocephalidae* and the *Anabantidae* in the Near East, where one species of the less specialized *Mastacembelidae* survived. *Mastacembelus haleppensis* C.V. is reported from Aleppo and the Upper Tigris (28; 60). The characters of this species seem to point to a close oriental relationship (9).

2. The composition of the Palestinian freshwater fish fauna.

As has been demonstrated the fish fauna of the Near East has many bonds with an older oriental stock. Because of its geographic position, Palestine shows much more of the oriental influence than Anatolia. Anatolia has its share of oriental elements (33; 34), but other geographic regions have also made considerable contributions to its fish fauna. Conversely, the West Asiatic and the Circum-mediterranean fauna, of which the first is prominent among Anatolian fishes, furnished only few genera (2 and 1, respectively, out of 12 foreign genera) to the Palestinian fish fauna. Quaternary acquisitions of the fish fauna are numerous in the Anatolian area; but one genus only of the Palestinian fishes (*Phoxinellus*) probably belongs to that group. Palestine's geographic position also favoured colonization from Africa, no traces of which can be found in Anatolia: 4 African species are living in Palestine (one of *Clarias*, 3 of *Tilapia*); 2 of its genera are of African origin (*Tilapia* and *Haplochromis*). Also, elements of marine origin are found (*Aphanius, Blennius*). Finally, endemics play a conspicious role in the Palestinian fish fauna. The genus *Tristramella* is endemic in the Syro-Palestinian area. Of about 24 species of fishes found in Palestine, 10 or more may be entirely confined to that country; to them a few endemic subspecies are to be added. One may surmise that the evolution of endemic species and subspecies has filled and is still filling free ecological niches. Everything seems to indicate that the Pliocene fish fauna of Palestine was much more diversified than the recent one. Geophysical events since then were in part markedly destructive. The adaptability of the fishes concerned could not keep pace with the changes of the milieu. But changes of conditions not only destroyed many old niches, they also created new ones. A relative stabilization of factors began probably when the number of species was at a low allowing for a steady increase which still continues; it possibly has become the prevailing trend of the prensent time.

3. The geographic distribution of freshwater fishes within Palestine.

The attempt to review the distribution of the fishes in the freshwaters of Palestine is seriously hampered by the lack of reliable data regarding the fauna of the coastal rivers. Most of the efforts of faunistic ichthyology has been spent on studying the fishes of the Jordan System. No detailed account will be given of those species which are either reported only once (*Barbus beddomi*, *B. continii*, *Varicorhinus sauvagei*), or whose identity is not beyond doubt (*Phoxinellus zeregi*, *Nemachilus leontina*); all of these are on record as caught in Lake Tiberias and have therefore been attributed to the endemic fauna of the Jordan System.

Only two fishes are known to be living exclusively in coastal rivers, *Aphanius fasciatus* and *Blennius spec. indet.* The first is

to freshwater; it probably moves in from the sea and back to it according to needs and conditions [33]. The *Blennius*, however, appears to be adapted to freshwater so much that it stays there permanently. A census of fish species in the few coastal rivers of Palestine has never been conducted. Besides the two species mentioned occasional catches have contained only such species as are also found in the Jordan River System. There is, therefore, no doubt, that a considerable part of the freshwater fishes of Palestine are common to the waters east and west of the country's principal water shed.

The coastal rivers naturally harbour a number of actually marine fishes which penetrate more or less regularly upstream for varying distances. These, too, are far from being well known. Among the numerous diadromous fishes (44) are the common eel, *Anguilla anguilla* (L), and several species of *Mugil*.

The differences between the fish fauna of the coastal rivers and that of the Jordan System are not yet understood. It is, first of all, the lack of detailed knowledge of the changing physiography of lake and river systems in the Pliocene and Pleistocene that makes it impossible to evaluate the conditions for migratory movements within the country. How many of the fishes found in the Jordan System are true endemics of that river, is unknown as a result of our incomplete knowledge of coast-river fishes. A few points may however be accepted as fairly sure. No species of the genus *Tristramella* —wholly Palestino-Syrian— is found in any of the coast rivers. The same is true of *Haplochromis flavii-josephi*, representing an African genus, and of *Nemachilus galilaeus*, an endemic species of an originally oriental genus.

It has long been recognized that the Jordan Valley is an important center of speciation not only of fishes. Peculiar ecological conditions are dominant in several localities. It will be no mistake to attribute much importance to Pleistocene volcanism which resulted in the upwelling of thermal springs in many places. Before emerging at the surface the spring waters pass rocks containing various amounts of soluble mineral substances (54; 80). It has been calculated that the numerous springs pouring their water into Lake Tiberias and into the Jordan tributaries south of it account for almost all of the mineral contents of the Dead Sea. High quantities of Ca, SO_4 and Br distinguish several of the most important springs. Radioactivity is also known to be one of the characteristics of several of those water sources. No doubt, various combinations of high temperature, chemical composition, and radioactivity of the water play a role in the speciation process.

In this connection it is worth repeating that Lake Tiberias is

[33] Belonging to a family of secondary freshwater fishes (43) *A. fasciatus* can not be classified as a truly migratory fish (44). It is not impossible that it is of the euryhaline type of the American *Fundulus heteroclitus* which seems to behave similarly.

inhabited by the following fishes which are absent from Lake Huleh: *Blennius vulgaris, Haplochromis flavii-josephi, Tristramella sacra, Tristramella simonis simonis.* Whether the overall situation adds significance to the records from Lake Tiberias of *Barbus beddomi, B. continii,* and *Varicorhinus sauvagei* [34] shall not be decided here.

The fish fauna of Lake Huleh is evidently poorer than that of Lake Tiberias. *Tristramella simonis intermedia* is the only endemic species of Lake Huleh [35]. Factors favouring speciation in Lake Tiberias, but absent from the Huleh area, may, however, not be solely responsible for this difference. The ecological changes setting in in Lake Huleh subsequent to its separation from the Tiberias basin have probably had a deteriorating influence on the fish fauna. From a limnological point of view the two lakes are strikingly different in character. Lake Huleh is a small and very shallow water body, bordered by Papyrus swamps and nourished by the cool waters of the Upper Jordan System; Lake Tiberias is a much larger water body, many times deeper, warmer and more constant in water temperature, nowhere swampy, and much poorer in supply of organic matter than Lake Huleh. It is to be regretted that we have no information about the ecological requirements of the fishes absent from Lake Huleh. The question could perhaps be studied experimentally whether Lake Huleh can provide the conditions necessary for survival and propagation of those species.

Appendix. Importations.

During the past thirty years a few fish species have been introduced into the freshwaters of Palestine for various reasons. *Gambusia affinis* (BAIRD and GIRARD) has been brought after the first world war in order to assist in the control of mosquitoes. It is now scattered practically all over the country. *Cyprinus carpio* L. has been imported and placed in artificial fish ponds from which it escaped into natural waters; it has also been set free in the lakes. There it has established itself more or less firmly and breeding has been observed. An imported trout, supposedly a hybrid of *Salmo irideus* GIBBONS with one or more close relatives, has been hatched for several years in a special station using the cool Jordan head waters. Adult specimens have been caught several times in the river, but it is not known whether the species reproduces there. *Tinca tinca* (L.) is the latest import. Kept in artificial ponds which are connected with open rivers it also has a chance to escape into free waters. It, then, remains to be seen to what extent it will succeed there. To date, *Gambusia* and the carp are the only imported fishes that have definitely become part of our fish fauna.

34 Possibly also to that of the questioned *Nemachilus leontina*.

35 That this fish is but infrequently found in Lake Tiberais is due to the topographic relations of the two lakes. The height difference between them is about 280 m, the horizontal distance about 16 km. Torrential waters of the rainy season are easily

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Zoogeography of the Near East

CURT KOSSWIG

EVEN though Anatolia (that is, Asia Minor and the neighboring eastern region called East Anatolia, in so far as it is a part of the Turkish Republic) can be included in the Palaearctic region, the number of faunistic elements of other than Palaearctic origin and/or distribution is highly remarkable. The same is true for Syria and Palestine, although the influence of Oriental and Aethiopian elements is much more noticeable in Palestine than in Anatolia. This means that there is a gradient from north to south for Palaearctic forms in the region in question.

It seems quite natural that in the distribution of animals there is not a clear-cut faunistic boundary but merely a more or less gliding transition from the center of one faunistic region to that of another. Unfortunately, how much significance an author is ready to attribute to the transitional character of a given region is a question of rather subjective judgement. From the point of view of the zoogeographer interested in Lepidoptera it may be justifiable to deny the transitional character of the Anatolia-Palestine region because the dominance of Palaearctic elements even down to North Africa is so well established that the intermingling into this fauna of some Aethiopian wandering species or of Eremian forms in the warm steppes or the deserts of this zone can practically be neglected. For the modern lepidopterist only the distribution of the different subspecies of a certain species is of importance; the area occupied by the different subspecies is, most probably, the result of the postglacial expansion from some refuges during the glaciation. De Lattin (1951-1952) worked out this interesting problem with great care and success.

It is easily understandable that the degree of certainty in reconstructing the historical geography of an area or of a species rises with approximation to present-day conditions. The more we have to refer to the geological past for the understanding of the present distribution of a systematic unit, the more hypothetical becomes our reconstruction of the probable historical course of events. At the same time, a higher degree of systematic independence among the forms compared means a diminished probability that their groupings are really natural. Whereas it can be taken for granted that all subspecies of one modern species are derived from one common ancestor, we can never be so sure when we compare different species or higher systematic units. In the ideal case a good (that is, a natural) system has to correspond to the degree of natural affinity; but we have to admit that in many cases there is still uncertainty about the natural relationship between species included in the same genus or between genera included in the same family. There are, however, many examples in which, for the understanding of the present distribution of a systematic unit, not the degree of relationship between certain members of this unit but the area covered by it actually and/or in the past is of primary importance. Fortunately in many such cases, facts concerning the biology and ecology of the form or group under investigation can be used as complementary to our deficient or uncertain systematic knowledge. The following pages may be understood from this point of view.

Faunal Boundary

A relatively sharp boundary between a fauna with many typically Palaearctic representatives and another of different faunistic relationship can be observed th

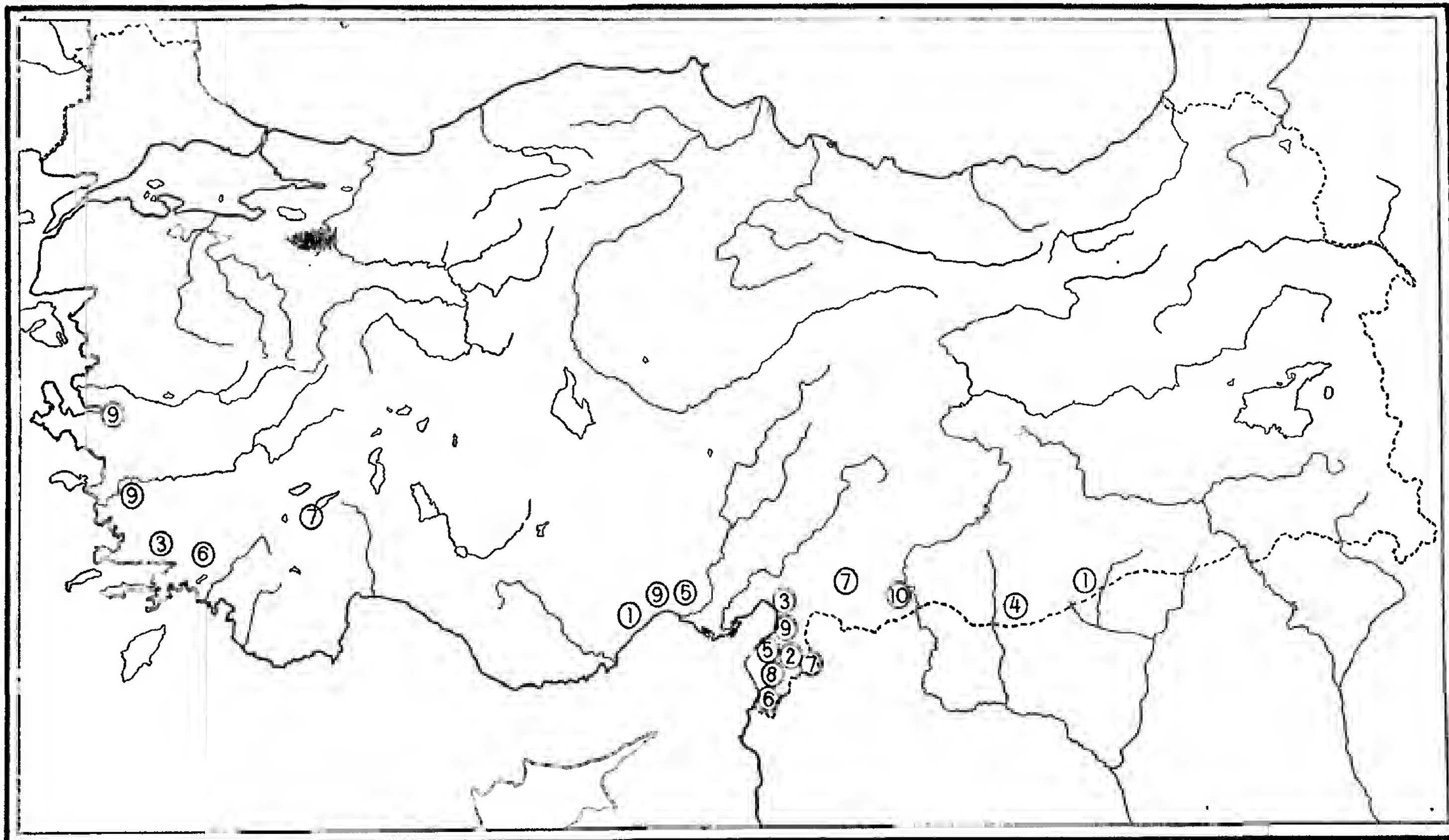


FIG. 1. Distribution of species of preferentially tropical distribution. 1. Driver ant, *Dorylus punicus*. 2–4. mammals: 2. *Rousettus aegyptus;* 3. *Herpestes ichneumon;* 4. *Gazella dorcas*. 5–8 and 10. birds: 5. *Pycnonotus xanthopygus;* 6. *Halcyon smyrnensis;* 7. *Ceryle rudis;* 8. *Anhinga rufa* (*chantrei*); 10. *Comatibis eremita*. 9. Chamaeleon (*Chamaeleo chamaeleo*).

moment we enter the plains south of the Toros mountains (Fig. 12). Suddenly one feels oneself in a foreign country, among an unfamiliar fauna from the central or eastern Anatolian steppes, or from the mountainous regions of northern, eastern, or western Anatolia. Animals such as driver ants (*Dorylus punicus*), fruit-eating bats (*Rousettus aegyptus*), the mysterious darter (*Anhinga rufa chantrei*), bülbüls (*Pycnonotus xanthopygus*), soft-skinned tortoises (*Trionyx euphratica*), a large monitor (*Varanus griseus*), the mongoose (*Herpestes ichneumon*), the saphan of the Bible (*Hyrax syriacus*), and many other species well known in Palestine find their northern limit on the southern slopes of the Toros mountains. We have good reason to assume that these species are newcomers in the south Anatolian fauna, having intruded into the north as late as the end of the glacial epoch. The specific and racial identity of many of these elements, with their congeners in Palestine and farther to the south, in Africa or in India proves this fact. (Figs. 1, 2.)

On the other hand, as a result of a movement towards the south in the glacial (pluvial) periods, some species that are widely distributed in Anatolia and even more in the north, e.g. in the Caucasus, the Balkans, Alps, or Central Europe, still exist in Syria and/or Palestine. Representatives of this element of more northern origin are, among others (Bodenheimer, 1935), the fire salamander, *Salamandra salamandra*, the newt *Tritu-*

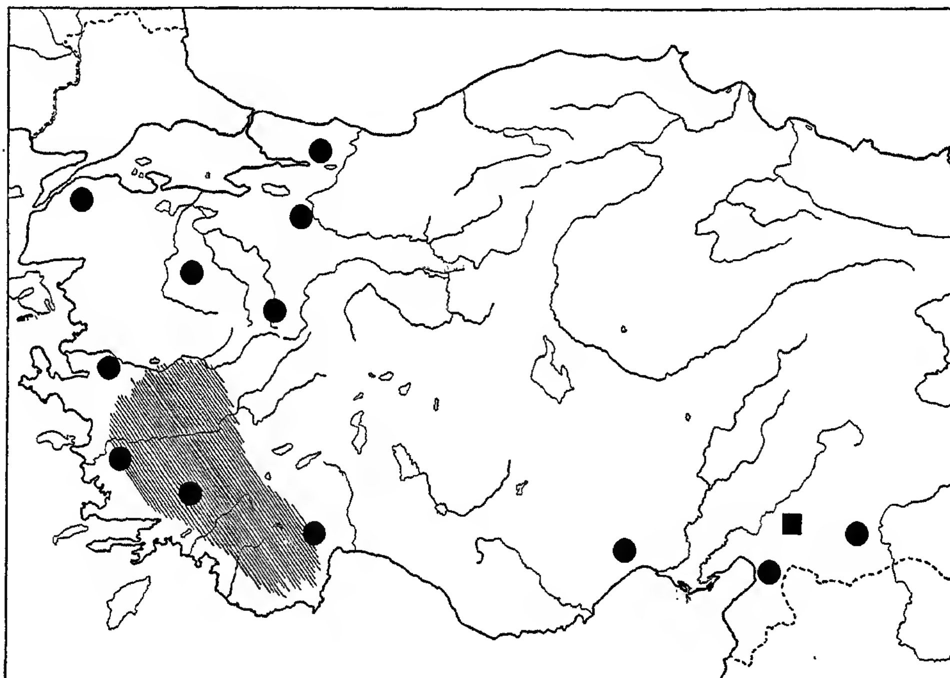


FIG. 2. Warmth-loving mammals in Anatolia. *Hystrix hirsutirostris* is indicated by circles. The area of *Felis pardus tullianus* is indicated by shading; one place at the eastern border of Asia Minor is indicated by a square.

rus vittatus, in earlier times the roe deer, and even some freshwater fish like *Alburnus, Rutilus,* and *Cobitis* (Fig. 3). Other intruders of northern origin, the Angara element, arrived together with the forms preferring cold and humidity mentioned above. The Angara element confronts us with species of the cold steppes of eastern Siberia which in glacial times easily gained distribution towards the west and from there also to the south. Grasshoppers of the genera *Stenobothrus* and *Chorthippus,* well represented in Anatolia, in the steppes as well as in the high mountainous regions, can be cited here. They can be found in some forms as far to the south as Palestine. Some other animals of Palaearctic origin, carabid beetles for example, and an earwig of the *Forficula tomis* group even reached tropical Africa where they are mostly confined today to the high mountain regions of East Africa.

The southern movement to Africa in glacial-pluvial times was facilitated by some land-bridges between the Palaearctic and Aethiopian regions, of which the one going through Syria and Palestine seems to have been very important. As a general rule we can state that there is a gradient from north to south in such a way that the Palaearctic forms become rarer the further we go towards the south. Today there are some discontinuities in this gradient caused by local ecological situations in certain regions that were passable in former periods.

An inverse gradient from south to north exists for tropical elements, and in this case again local ecological reasons rather than historical ones seem to have determined the absence of some forms, where their existence could be expected. For example, the fact that no mouth-breeding cichlid fish (*Tristramella*) can be found in the lake of Antiochia, whereas they exist in Aleppo, may be caused, not by the restricted mobility of these fish, but by some special ecological factor not known to us as yet.

This exchange of representatives of land and freshwater faunas of different origin, the one coming from the modern tropics, the other developing in the Palaearctic, began in the Pliocene. In this geological period the last communication between the Mediterranean Sea and the Indian Ocean, the so-called Syrian-Iranian Sea, retired completely, allowing the migration farther to the south, and conversely to the north, of land and freshwater animals. Until the desiccation of the Syrian-Iranian Sea, the Anatolian fauna developed primarily as a part of the Palaearctic fauna. Bodenheimer suggests (1935) in a more special sense that a great part of the Anatolian fauna in the Tertiary derived from what he calls the Atlantic fauna, in which the Mediterranean region and some of the Atlantic islands are to be included. In fact, there is a most remarkable similarity in the composition of the faunal elements in Anatolia, the peri-Mediterranean and the sub-Mediterranean regions, especially in groups with restricted mobility like millipedes, woodlice (Verhoeff, 1940, 1941*a*, 1941*b*), and also others. Families of animals of slow mobility, active or passive, such as the millipedes, offer an excellent material for historical zoogeography (Kosswig, 1943). In contrast to the millipedes of Anatolia, which show a preponderant Palaearctic, Mediterranean, or sub-Mediterranean, relationship, those of Palestine reveal relations also with Africa by the presence of spirostreptids completely absent even in the most southern regions of Turkey. But it seems worth mentioning that a remarkably high number of the diplopods of Palestine show near relationship with those of the Caucasus and of Anatolia (e.g. genera *Amblyiulus, Brölemannia, Lysiopetalum*). The distribution towards the south of these elements is nearly in correspondence with that of the genera *Salamandra* and *Triturus.* In the southernmost corner of Turkey, in the Sandjak of Iskenderun a glomerid was found which has its nearest relative (Dr. Lohmander in litt.) in *Albanoglomis,* a western Balkan genus.

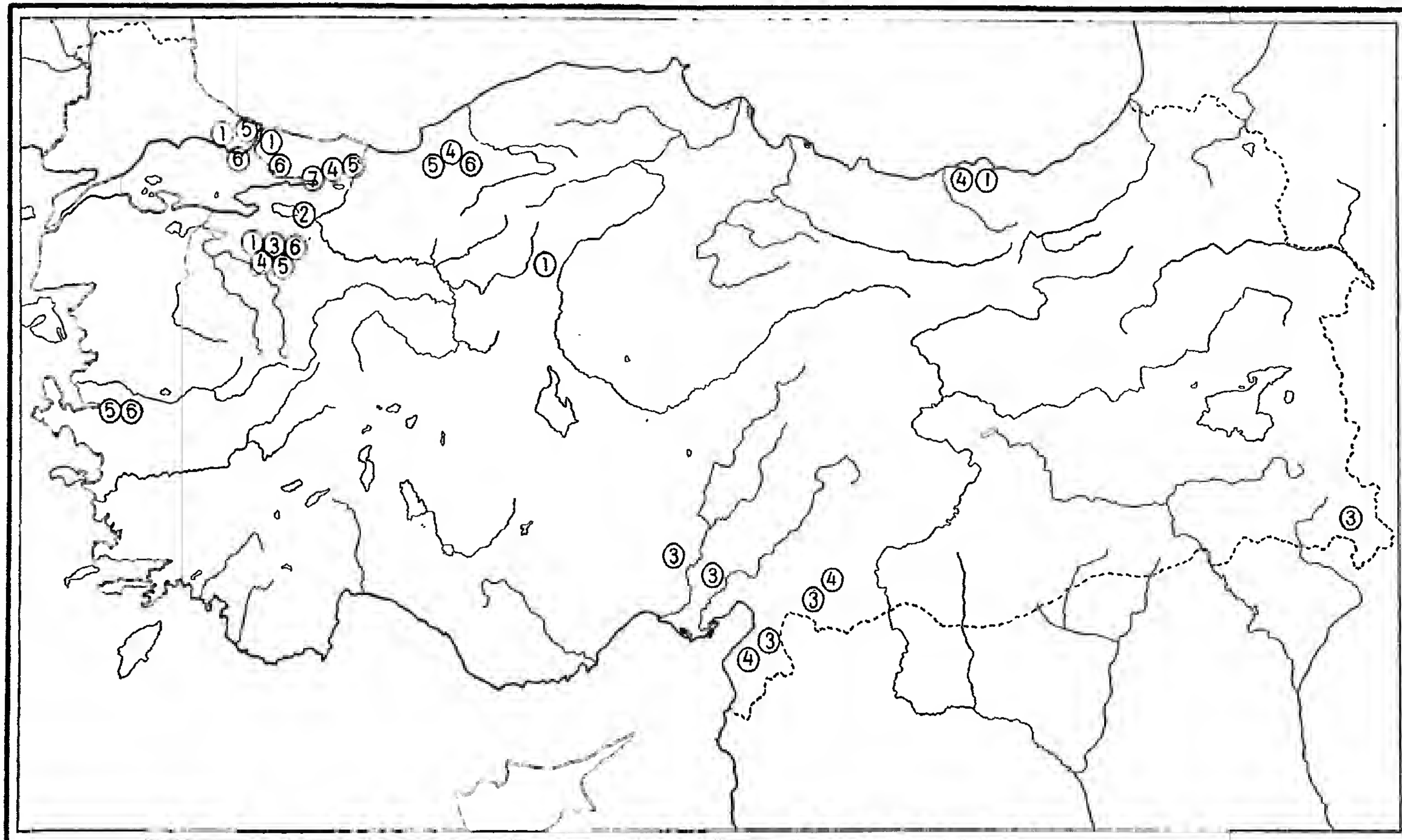


FIG. 3. Reptiles and amphibians of preferentially northern distribution in Anatolia. 1. *Anguis fragilis;* 2. *Vipera berus;* 3. *Salamandra salamandra;* 4. *Triturus vittatus;* 5. *T. cristatus* (*Karelini*); 6. *T. vulgaris;* 7. *Bombina bombina.*

FIG. 4. The Arboreal and the Eremial in modern Anatolia. Stippled areas are steppes; large alpine zones are indicated by hatching, and small alpine areas in solid black. The rest of Anatolia was originally covered by forests which persist even today in the form of single

ZOOGEOGRAPHY*

ZOOGEOGRAPHY is a discipline of Zoological Science which requires for its study a thorough knowledge of animal systematics and behaviour; animal ecology; geography, both past and present; climatology, both past and present; palæontology and geology. It is, in fact, an endeavour and not a science in its strict sense, for, however advanced our knowledge of zoogeography may be of any particular region, a considerable amount of speculation must continue to exist in zoogeographical treatises. Prof. L. F. de Beaufort, formerly Director of the Zoological Museum and Professor of Zoogeography at Amsterdam, has done a great service to zoology by embodying his vast knowledge and experience of zoogeographical studies in a readable text-book on the subject. So far, mammals and birds have received the greatest attention in animal geography and though sometimes other terrestrial groups of animals also received attention, inland aquatic faunas had been practically ignored. Prof. de Beaufort's book, even in its title, now lays an emphasis on inland waters which is a welcome departure from earlier works and gives a proper perspective to the subject.

In a short preface, the author thus defines the scope of the work: "Zoogeography of the land and of inland waters as discussed in this book, is principally historic zoogeography, that is to say that the factors influencing present land and freshwater distribution have mostly been effective in the past. But, as in all sciences built on history, such as palæogeography and phylogeny, much is hypothesis, and ever since its infancy historic zoogeography has been looked upon with misgiving by many zoologists. The fault lies with those zoogeographers who have been too rash in building land bridges over oceans or sinking whole continents into the depths of the sea without giving thought to the geological possibilities of such catastrophes."

The greatest fascination of zoogeography lies in an endeavour "to explain the present from the past, or, *vice versa*, to reconstruct the past from the present". Though it may seem simple, it is a very painstaking task. For instance, even the present distribution of a species depends on (*i*) the age of the species, the older the species the greater is likely to be the range of its distribution, (*ii*) the possibilities of its dispersal depending on ecological factors, both biological and physical and (*iii*) the possibilities of its dispersal in the past depending on palæoclimates and palæogeographical features of the country. It is very rightly stated by the author that to build the future edifice of zoogeographical science, one should look to genera or species specialists, for only they can provide the reliable data of distribution through a correct appreciation of speciation.

The author has made it clear and the fact is worth remembering by all zoogeographers that the dispersal of land and freshwater animals are governed by different factors, for many land animals will be able to use a narrow ridge rising out of the sea for crossing from one island to another whereas the same will not be possible in the case of freshwater animals, which will have to wait till the river systems of the two islands become connected.

"Progress in the dispersal of the freshwater fauna will thus be slower than that of land animals, and this difference in time may sometimes help us to form an opinion about the age of the connection."

There is an unlimited wealth of information for zoologists of the different parts of the world in the various chapters dealing with the Holarctic Region, the British Isles, the Oriental Region, the Ethiopian Region, Madagascar and the neighbouring islands, Neogaea, Notogaea and the Celebes, the Moluccas, and the Lesser Sunda Islands. All groups of animals have been given due attention and for the specialist it provides a very useful review of the knowledge upto 1947 or thereabouts.

The utility of this work would have been greatly increased if the author had paid some attention to the rate of speciation in various groups of animals under different ecological conditions. For instance, the author refers to the Malayan element in the fauna of Peninsular India and explains the discontinuous distribution of this fauna on the formation of the Deccan traps in the intervening areas. Taking the isolated fauna as a whole, it can safely be said that in the main the terrestrial isolates migrated during the pluvial periods of the Pleistocene and that the aquatic fauna may have been migrating during the Miocene and Pliocene also. The very highly specialised forms seem to have evolved and spread not earlier than the Pliocene. The formation of the Deccan traps, on the other hand, is stated to have commenced

* *Zoogeography of the Land and Inland Waters*, by Beaufort, L. F. de. (Text-Books of Animal Biology Series). Pp. viii × 208. Text-Figs. 10. (Messrs. Sidgwick and Jackson Limited, London), 1951, Price 30*sh*, net.

in the late Cretaceous and ended in the early Eocene.

Thus there can be no effect of the latter on the distribution of Malayan element in the fauna of Peninsular India. The Symposium on the Satpura Hypothesis, organised by the National Institute of Sciences of India, seems to have escaped the attention of the author. More data have recently been obtained in favour of the Satpura Hypothesis. The palæontological evidence with regard to the age of the genus *Thynnichthys* Bleeker as Eocene would seem to require a thorough checking.

It must be an oversight on the part of the author to state on page 36 that the "Cobitidæ are restricted to Europe and Asia" when he includes *Nemachilus* among the African fauna on page 103. The work is so closely packed with diversified material that such mistakes are likely to go undetected.

A useful bibliography of 132 references is included at the end of the work and there is a detailed index of 16 pages. The book is of a handy size, beautifully printed and got up. The Editor of the series, Prof. H. Munro Fox, the author and the publishers are to be congratulated on bringing out such a meritorious work of reference.

S. L. HORA.

INDIAN VETERINARY RESEARCH INSTITUTE—DIAMOND JUBILEE

THE Diamond Jubilee Celebration of the Indian Veterinary Research Institute, which was held on 11th March 1951, marks the culmination of 60 years of its useful service to the country. Inaugurating the function, the Hon'ble Shri. K. M. Munshi, Minister for Food and Agri-
country. Inaugurating the function, the Hon'ble

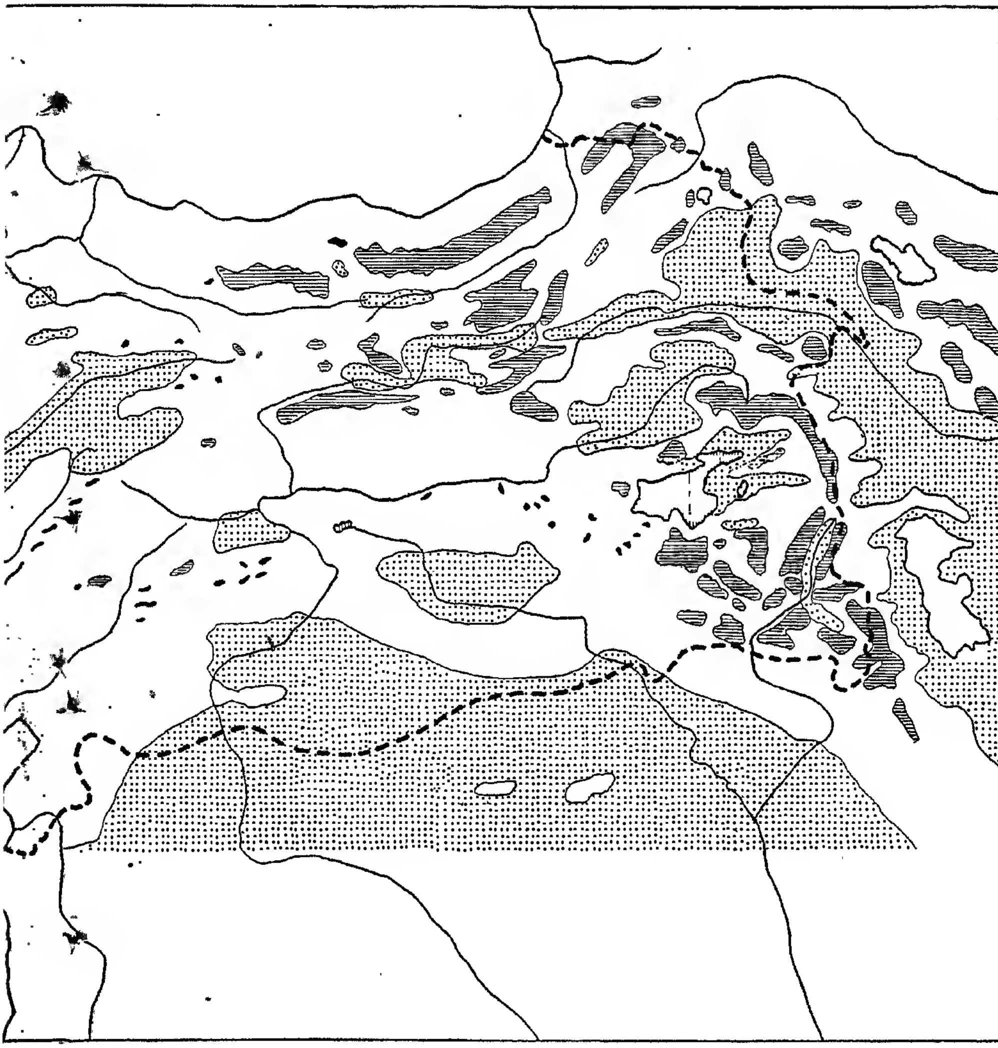
"India has one of the most important livestock industries of the world whose actual as well as potential value is considerable. She possesses 175 million cattle and buffaloes amounting to a quarter of the world's bovine population, in addition to millions of sheep, goats, poultry and other animals. Yet, the *per capita* production and consumption of milk in the country is, perhaps, the lowest in the world. It is said that this is due to adverse environmental conditions. We might therefore look to the I.V.R.I. and the Animal Husbandry Wing for improving these conditions so that the country can make full use of its livestock population. Effort in one direction alone will not be sufficient; what is required is a multipronged attack on the complicated problems. Breeding, proper management, feeding of livestock and disease control must be tackled in one comprehensive scheme which can no doubt be linked with the Grow More Food Campaign ultimately."

LADY TATA MEMORIAL TRUST
SCHOLARSHIPS AND GRANTS FOR THE YEAR 1951-52

THE Trustees of the Lady Tata Memorial Trust announce on the death anniversary of Lady Meherbai Dorabji Tata, 18th June 1951, the awards of Scholarships and Grants for the year 1951-52.

The International Awards of varying amounts (totalling £3,600) for research in diseases of the blood with special reference to Leucaemias are made to Doctors Pascou Atanasiu (France), J. Bichel (Denmark), George Discombe (England), Astrid Fagraeus and Bo. Thorell (jointly) (Sweden), Henri P. L. Febvre (France), Niels M. G. Harboe (Denmark), Charles Oberling (France), Gunther Schallock (Germany), J. B. G. Dausset (France), C. C. Ungley (England), and A. R. Gopal-Ayengar (India).

Indian Scholarships of Rs. 250 per month each for one year for scientific investigations having a bearing on the alleviation of human suffering from disease are awarded to Messrs. Samavedam Srinivasa Sriramacharyulu (Andhra), Gangagobinda Bhattacharya (Calcutta), Madhav Vinayak Patvardhan (Coonoor), Anant Vithal Sunthankar (Bombay), and Dr. (Miss) Smitha Popatlal Bharani (Bombay) and Miss Kamala Ramaswamy (Bombay)



trees or small groups of trees in regions where forests were destroyed by men and goats. Forests are well developed in the northern, western, and southern mountains; those on the coast of the Black Sea are humid, the others are dry forests. (Map drawn after Louis.)

Relations of Anatolian Fauna

Although the Mediterranean and sub-Mediterranean element is well represented in the Anatolian millipedes and other sedentary groups, we must keep in mind that just such Anatolian species with restricted active and passive mobility have clear faunal relations, not only with the west, but also with the east of the Palaearctic, even as far as China and Japan, e.g. the genus *Amblyiulus.* Thus, it seems, we are justified in seeing in the older faunal elements of Anatolia members of a widely distributed fauna of the warmer Tertiary which once occupied a nearly continuous area in the whole Palaearctic. This fauna differentiated in the course of millions of years into forms representing one another geographically and was partly destroyed, partly driven back into refuges, as a result of the progressive climatic changes with the approach of the Quaternary.

Many land and freshwater genera of this Palaearctic fauna of the Tertiary do not exist in Siberia today, whence refuge into a more moderate climate was impossible. Anatolia offered such refuges, one in the Aegean and western Anatolian zones, the other in eastern Anatolia. These two refuges were separated from one another by high mountains in the north and in the south, and by a large freshwater lake or a system of lakes which covered an area as great as that from the sources of the Great Meander to the eastern border of Asia Minor. Although Anatolia towards the end of the Tertiary was raised up from nearly sea-level to an altitude of approximately 1000 metres, and in spite of the postglacial steppification of central Anatolia on the one hand and of the highlands around Mt. Ararat (Louis, 1939) on the other, the majority of its animals are forms of the Palaearctic Arboreal (Fig. 4). They have been settled there since the Tertiary or at least since the Quaternary. With the amelioration of the climate in postglacial times, many species of the latter group reoccupied the territories in central Europe where they were lost in the glacial period. As was mentioned above, the pumping action of the glacial period was of great importance for the mixing of northern species with the fauna of Syria, Palestine, and Africa south of the Sahara (Figs. 5, 6).

Even though the Anatolian fauna shows clear relations with that of the Palaearctic, it must be admitted that some of its species do not fit in with this rule. These forms cannot be regarded as members of a more southern fauna which arrived in southern Anatolia after the glacial epoch; it even seems very doubtful whether these forms have come into Anatolia only after the desiccation of the Syrian-Iranian Sea in the Pliocene. I should like to mention here only some examples of these old elements, which may be called Gondwanian forms. They show faunal relations between Anatolia and regions far remote in the south, these regions being separated from the major part of the Gondwana continent in such early periods as the Secondary or the beginning of the Tertiary.

Among the Anatolian millipedes the genus *Melaphe* (Attems, 1943), is to be discussed. Its area of distribution includes Albania, Thrace, Anatolia, Mauretania, and Abyssinia. The generally low mobility of millipedes and the ecological needs of *Melaphe* in particular make it improbable that the area of distribution of the genus is the result of migrations in the recent past. If we add that the most closely related genus to *Melaphe* is *Karakodesmus* in Venezuela, it sounds preferable to describe *Melaphe* as an ancient type of Gondwana origin. The same interpretation can be given to the close relationship of the blind and cavernicolous beetle *Cereaxina troglodytes* of south Anatolia (Jeannel, 1934) with the highly specialized and myrmecophilous genus *Lioclemmus* of Madagascar. The relationship of a Mediterranean and Anatolian genus of locusts, *Saga,* to genera in South Africa and Australia is an argument under the

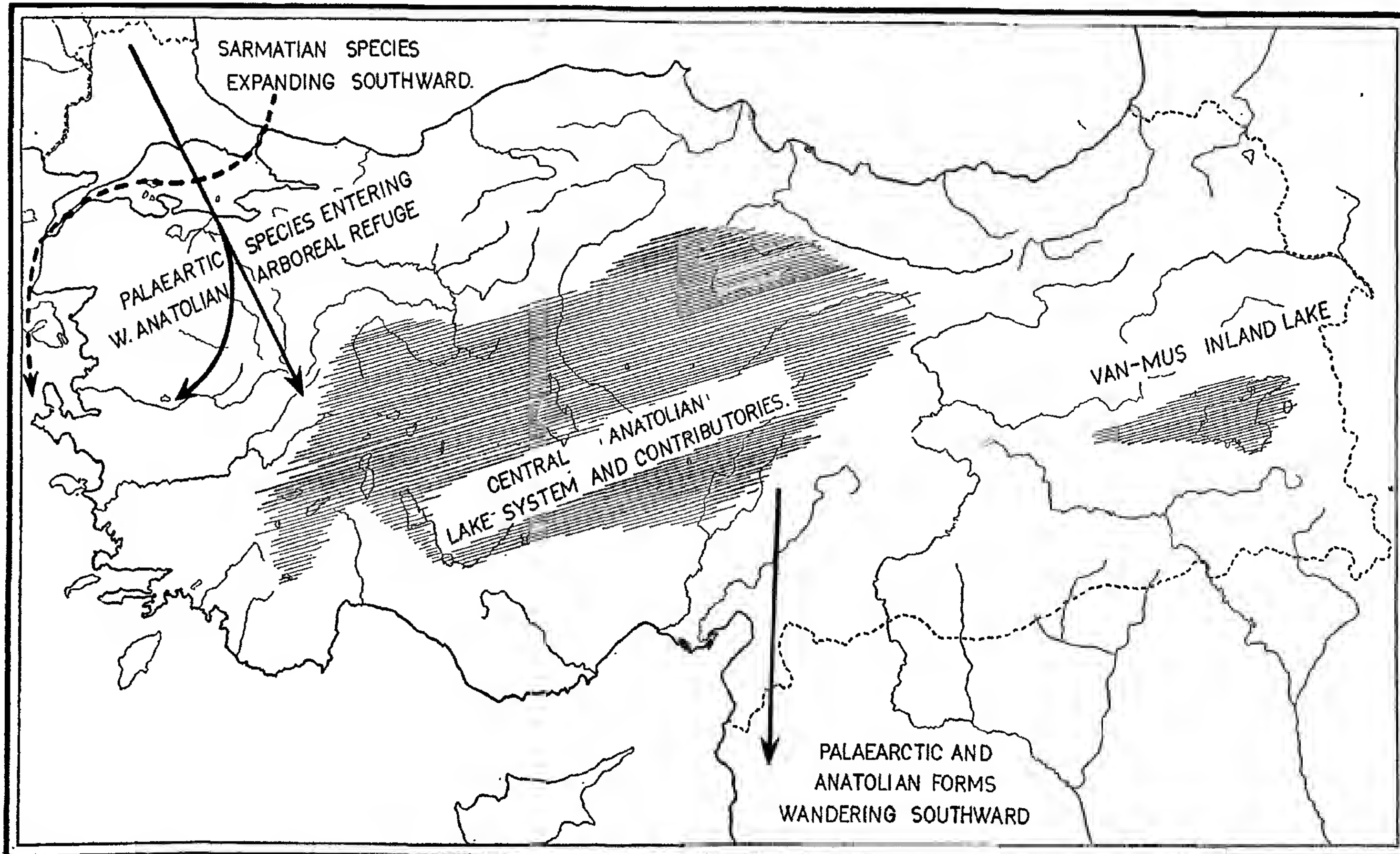


Fig. 5. Movements of the Anatolian fauna during the glaciations.

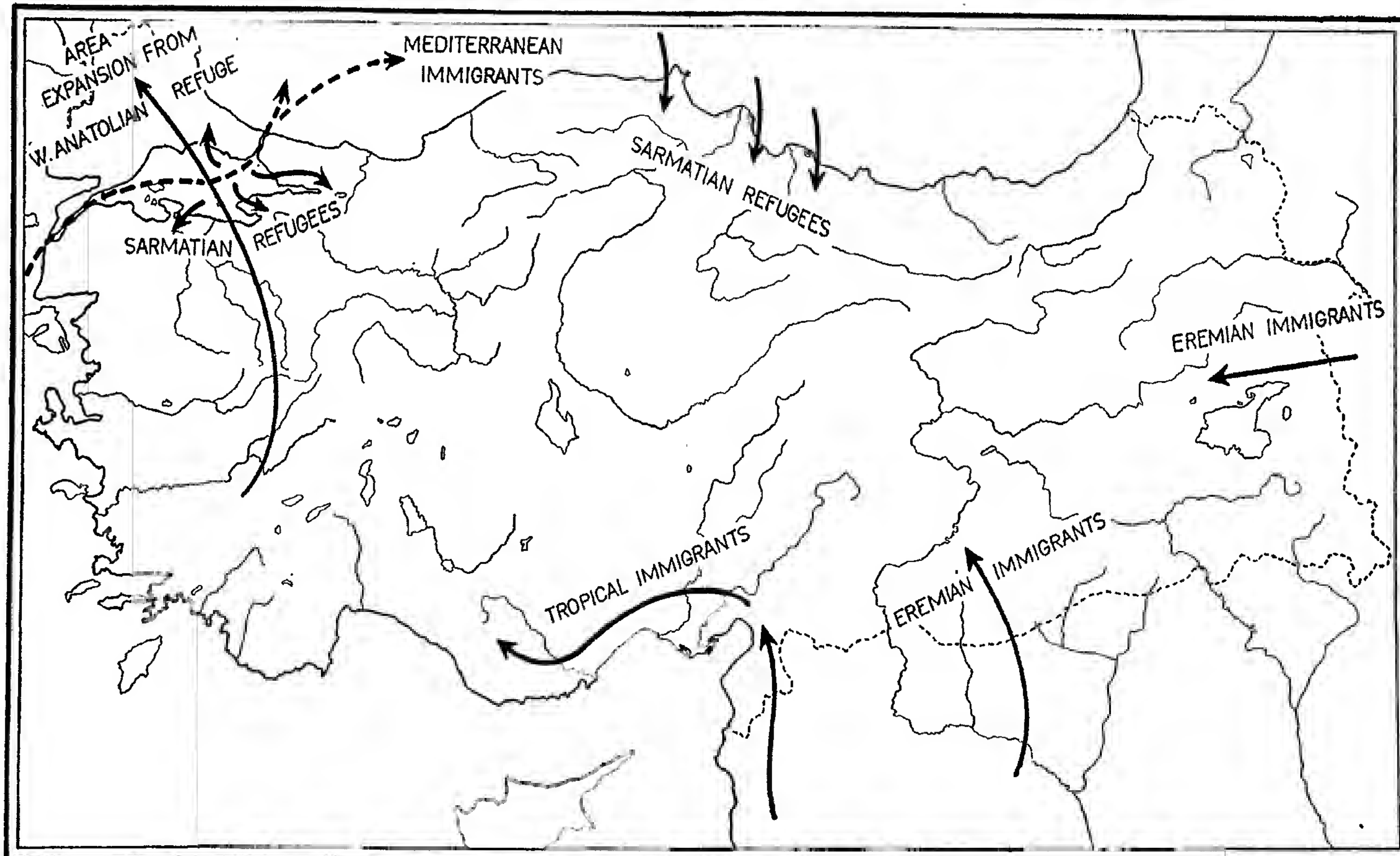


FIG. 6. Movements of the fauna in the postglacial period.

same heading. Finally, the remarkable case of the wingless earwig genus *Pseudisolabis* (Burr, 1947) may be mentioned. This genus has one species in New Zealand, which was separated from Australia in the Mesozoic, some others in Australia, Malaya, and India, and a new one recently described from western Anatolia. The presence of members of these Anatolian genera in widely removed and early separated regions of the southern hemisphere indicates the great phylogenetic age of these forms. But on account of the rareness of these examples and our deficient knowledge of geological relations in the remote past, we cannot as yet work out the history of such species in more detail.

The faunistic relations between the Far East and Anatolia can be proved by many examples from different groups of animals. They form only a small part of the very large mass of material by which the existence of a much higher uniformity of the Palaearctic fauna (and flora) during the warmer Tertiary can be shown. Contrariwise, the relations between the Nearctic and the Anatolian fauna are more or less sporadic. Nevertheless there are some highly remarkable cases by which such a relation can be shown. It has long been known that the woodlice *Mesoponorthus* are represented by one species in Middle America, and that the subgenus *Collaria* of the centipede *Scolopendra,* with many Mediterranean and one Anatolian species, has one member in Mexico. Recently another interesting case was found by Chamberlin (1952). The centipede family Gosibiidae which up to now was thought to be endemic in North America has two genera and nine species in Anatolia! (Fig. 7). The material presented as yet is not sufficient to decide by which path the distribution of these animals may have been accomplished. But it seems worth stating that the Nearctic-Anatolian relation is not indicated by cold-tolerant species which are distributed in north and east Asia and for which the use of the Bering bridge would be probable. Rather are we concerned with a relationship between animals adapted to life in the Mediterranean region and similar ones living in the Nearctic. In the case of *Mesoponorthus* a passive transport may have a low probability, but this mode of distribution seems completely improbable in the centipedes mentioned above.

Faunal Migrations

Our information is more adequate in the case of the immigrants into Anatolia from the south during the Pliocene. The best-known facts about this faunal migration are those concerning the distribution of freshwater fishes from India to Anatolia and also to Africa. The African freshwater fish fauna contains a group of forms, the characids, with clear relations to South America, besides an old and endemic element of mormyrids, bichirs, phractolaemids and others. As a result of a long divergent evolution after the early isolation of Africa from South America by the Atlantic Ocean, these elements, systematically, are considerably remote from one another. A third group of African freshwater fishes has very close systematic relationship with those of India (Kosswig, 1954*b*), for instance the genera *Barilius, Discognathus, Barbus, Clarias, Mastacembelus,* and many others. The generic identity of this third group in India and in Africa supports the hypothesis that these elements were exchanged recently, not earlier than in the Pliocene (Steinitz, 1954). There are good reasons to suppose that a more indirect route—the north Arabian-Syrian—was used for the invasion of Indian genera into Africa. This means that the tropical Indian fishes passing Syria and northern Arabia came into the neighborhood of Anatolia, which they entered freely. Some of these forms, e.g. an endemic subgenus of *Tylognathus* in western Anatolia, are still remnants of this tropical invasion from India (Figs. 8, 9.). The greater part of these Indian invaders went further to the south, leaving their traces in Palestine too. The reason

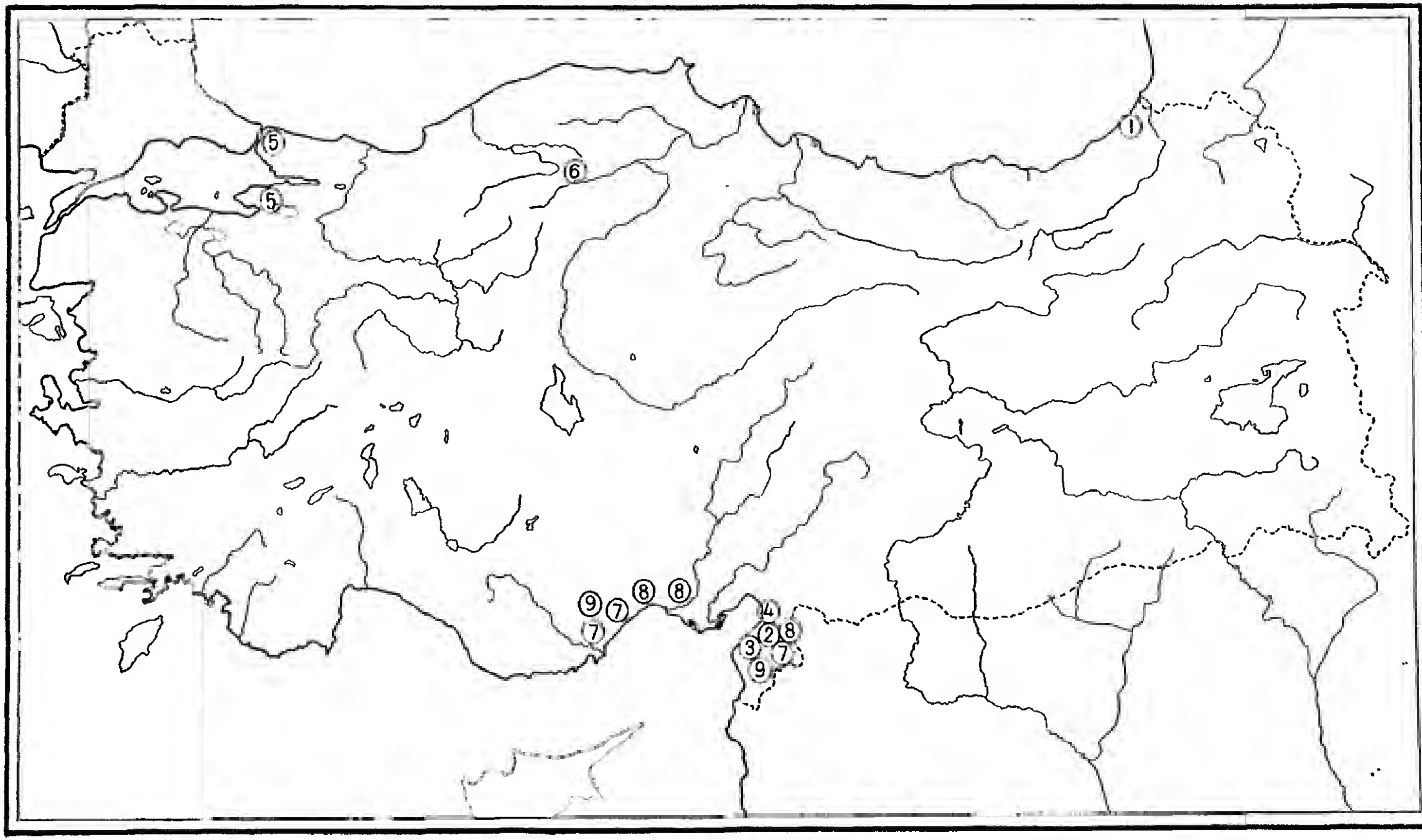


Fig. 7. Gosibiid Chilopoda in Anatolia (the family was once thought to be completely North American). 1. *Ottobius hopanus;* 2. *Turkobius adherens;* 3. *T. annexus;* 4. *T. errantus;* 5. *T. orientis;* 6. *T. plesius;* 7. *T. andrethus;* 8. *T. sogukolukus;* 9. *T. ocellatus.*

why the invasion was unilateral and why no African forms migrated in the inverse direction into India cannot be answered today. But it seems worth mentioning that such African forms as reached western Asia are also known from Palestine and Syria; this means that these forms also took the longer northern route instead of the direct route to the east where the Indian Ocean, the Persian Gulf, etc. always formed a barrier to the direct expansion of freshwater animals.

Relics of the tropical invaders from India into the Anatolian freshwater fauna are rare today. This is easily understood from the fact that at the end of the Tertiary three main factors contributed to a destruction of biotopes suitable for their existence: (1) the climatic changes in the Glacial Age; (2) the desiccation of most of the central Anatolian lakes or their transformation into azoic salt lakes; (3) the elevation of the Anatolian plains to more than 1000 metres above sea level, which resulted in very hard winters. But there are some sufficiently warm refuges, as for instance, the lakes from which the Great Meander rises, where such interesting forms still persist and now live together with other species which are of a totally different origin. In the sources of the Great Meander, swarms of a new species of *Mesomysis* (Bacescu, 1948) live together with fish of Indian (e.g. *Tylognathus Klatti*), central European (e.g. *Gobio gobio*), southern European (e.g. *Pararhodeus*), and central Asiatic (e.g. *Acanthorutilus*) relationship. The crustacean mentioned above belongs to a genus the distribution of which was hitherto thought to be restricted to the basins formed by the separation of the Sarmatian Sea. This greatest inland sea of brackish to freshwater character of the second half of the Tertiary persists today in the form of three basins separated from one another: the Black Sea, the Caspian Sea, and the Aral Sea. The influence of the Sarmatian fauna on that of Anatolia was very important for relatively long periods (Kosswig, 1942; Kosswig and Battalgil, 1942). On one side the north Anatolian coast was bordered by the Sarmatian Sea, or rather, the two parts here concerned: the Euxine and the Dacian lakes. The former was saltier than the latter, and they were separated from one another by the Crimean land between the Podolian platform and Cape Bafra. As far as we can judge, the Dacian Lake was important for the faunal exchange between central Europe and Anatolia (Fig. 9). The Sarmatian Sea was joined to the Aegean lake system, which covered the territory of the modern Aegean Sea and ended in the Mediterranean near the island of Cos. The influence of central European species, the so-called Danube fauna, on the rivers Maritza, Struma, and Vardar, and in the territory of Greece and western Asia Minor, can easily be understood from this geographical circumstance (Kosswig, 1954*a*). This situation explains also the route followed by freshwater fishes of south European origin from Greece to Anatolia and vice versa. A system of rivers and lakes in the lowlands of the Aegean landmass favored the exchange of freshwater groups of animals. On the other hand, even in Tertiary or Quaternary times the Aegean lake system was a faunal barrier for animals of other ecological requirements than those of freshwater animals. For instance, the petraëic millipedes are quite different on the Asiatic and European sides of the Aegean Sea. The difference is certainly the result of a long period of isolation of the two sides by a territory the ecological make-up of which was an impassable boundary for them.

Although this interpretation seems very probable, we have to state that the presence of a number of central European and Sarmatian freshwater species or near relatives of them in Anatolia is not in accord with this assumption. The presence of *Alburnoides bipunctatus* in north Anatolian rivers flowing into the Black Sea *and* in the Euphrates, and of *Gobio gobio* in small rivers flowing into the Black Sea and also around the Great Salt Lake, are

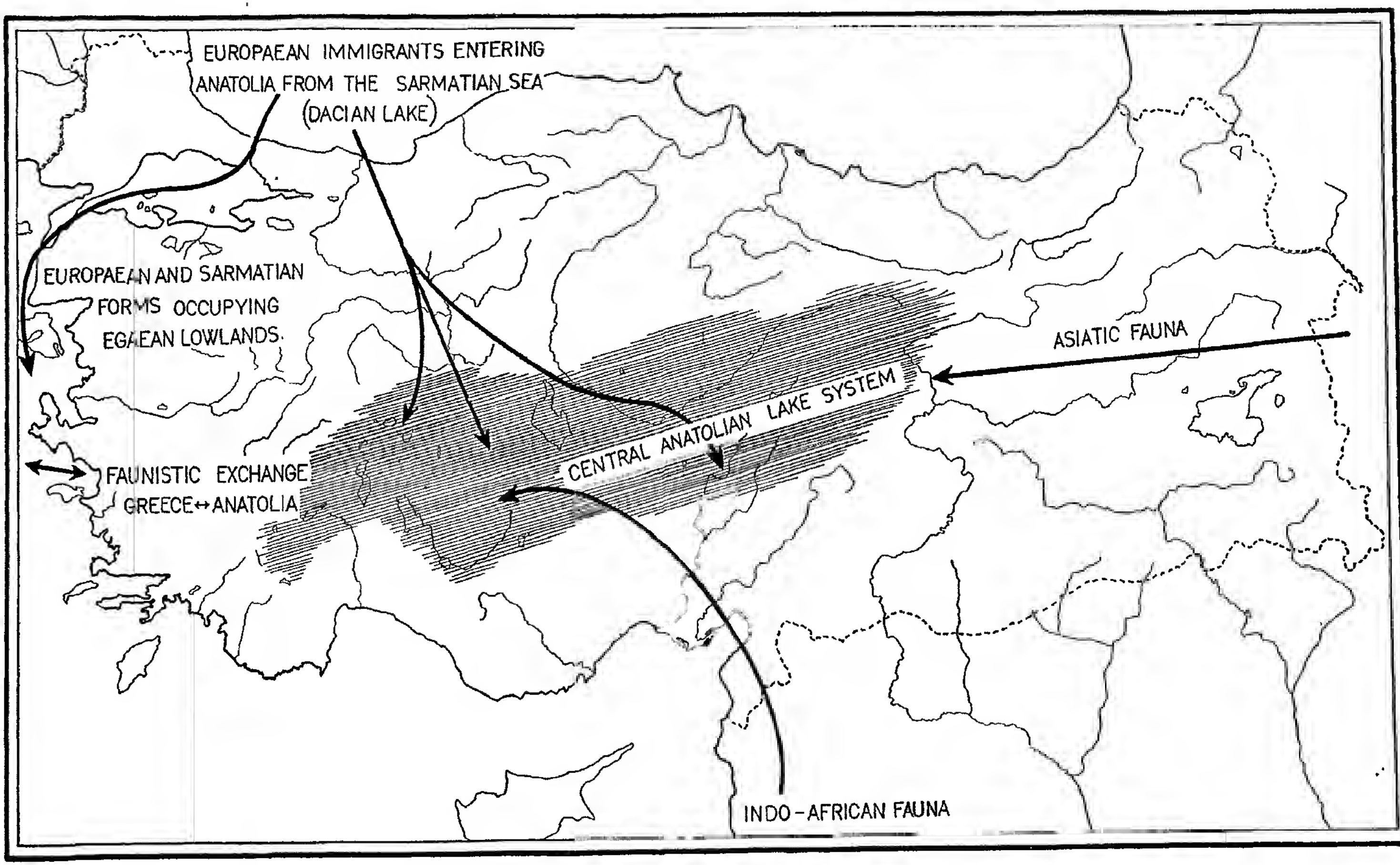


Fig. 8. Faunistic relations of the freshwater fauna in the Pliocene.

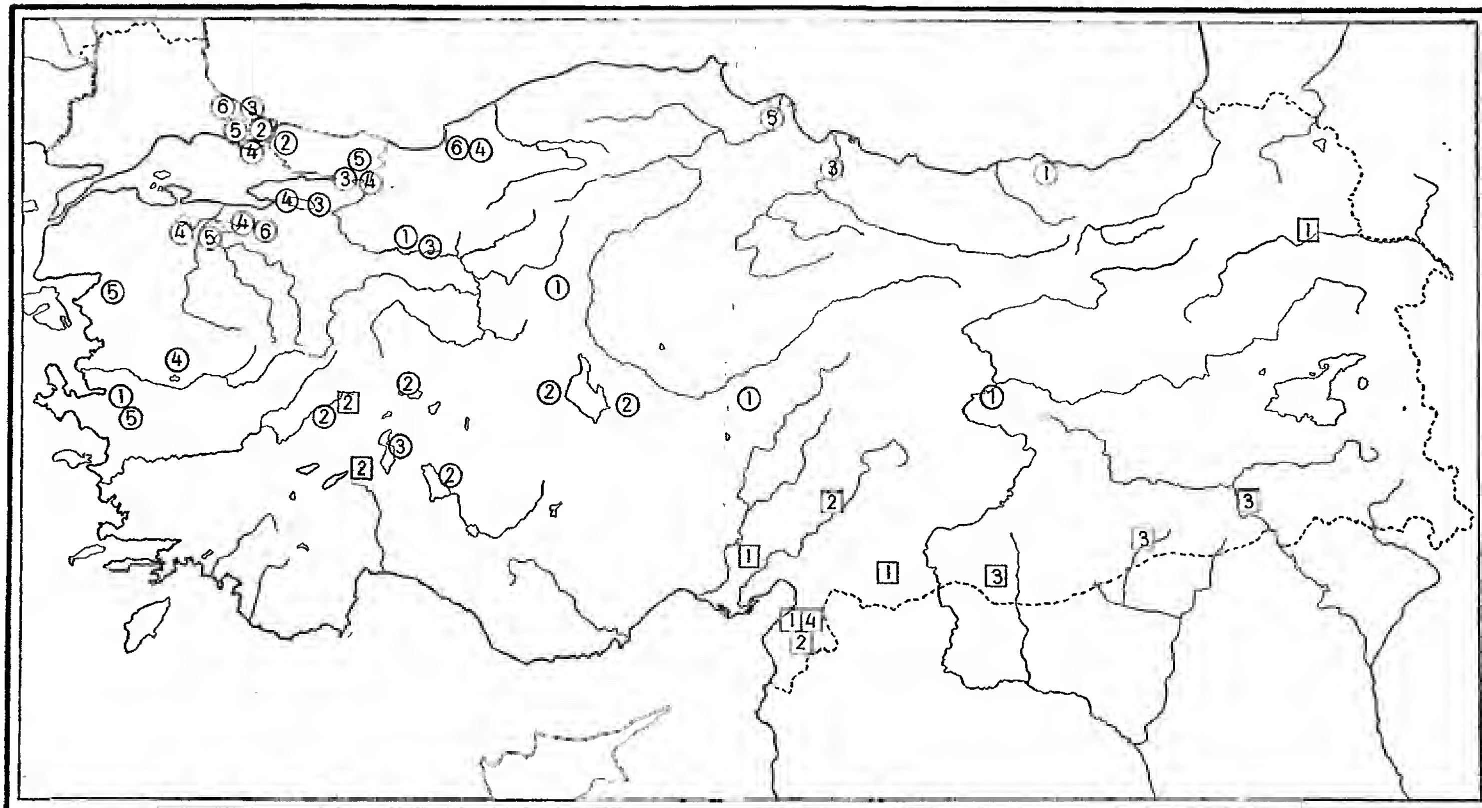


FIG. 9. Freshwater fishes of southern origin, indicated by numbers in rectangles, and fishes which are distributed also in central (eventually also in northern) Europe indicated by numbers in circles.

Southern species (in squares): 1. *Discognathus* (3 species); 2. *Tylognathus* (2 species); 3. *Mastacembelus halepensis;* 4. *Clarias lazera.*

Northern species (in circles): 1. *Alburnoides bipunctatus;* 2. *Gobio gobio;* 3. *Vimba vimba* (+ *tenella*); 4. *Chalcalburnus chalcoides;* 5. *Rhodeus sericeus;* 6. *Tinca tinca.*

facts under this heading. It is not very satisfying to regard these fishes as late invaders during the glacial period in which the invasion of elements of a more northern fauna into Anatolia was easy and actually accomplished by many species with good locomobility. The formation of a series of subpecies of *Gobio gobio* in central Anatolia and even of a closely related endemic species (*Gobio hethiticus*) indicates a longer period of stay of these elements in Anatolia. The presence of the remarkable Sarmatian genus *Mesomysis* in central Anatolia also requires another interpretation. It is quite impossible to assume that these small mysids which live in lakes wandered actively against the currents of rivers coming from the Anatolian high plateau and sending their waters into the glacial Black Sea. It is more probable that the genus arrived early, at a period when there was no great difference between the altitude of Anatolia and the sea level. Under these conditions a lake-dwelling species could actively extend its range. Such a situation can be imagined only in the Pliocene or earlier, i.e. in a period when the Asiatic freshwater fauna, especially the Indian forms, had just begun to enter Anatolia. We can therefore suppose that central European and Sarmatian species of the north Anatolia coast spread southwards by two routes: The one was via the Northern Marmara basin and the Aegean lowlands, a route which existed for a long time; it was restituted during each glaciation and interrupted during the interglacials when the Mediterranean covered this region, extending as far as the Black Sea. The other route lay further to the east, and it is by this route that Anatolia could be reached (Fig. 8).

After the breakdown of the Aegean continent in glacial times, the faunal exchange between Greece and Asia Minor ceased. By the newly formed Aegean Sea many species extended northwards from the Mediterranean into the Sea of Marmara and the Black Sea, which were at this time separated from the Caspian; in the Caspian the old Sarmatian fauna of brackish or fresh water has been able to persist up to the present, whereas in the Black Sea this Sarmatian element was partly destroyed and partly driven into the deltas of its great rivers or into lakes separated from the basin of the Black Sea itself. More than 75 per cent of the fish species of the Black Sea today are of Mediterranean origin (Slasdenenko, 1936). A number of species return for spawning into the Sea of Marmara (e.g. the mackerel, *Scomber scomber*) or even into the Mediterranean (e.g. the tunny, *Thunnus thynnus*) after having visited the rich feeding grounds of the Black Sea. The economic importance of the Bosphorus depends essentially upon the intensive fishing provided by the regularly migrating species, such as mackerel, bonito, and others.

Some species have adapted themselves completely to the conditions in the Black Sea and can in part be distinguished from their Mediterranean congeners (e.g. the anchovy, *Engraulis encrasicholus;* the gar pike *Belone belone,* and others). The bonito (Nümann, 1953) shows extraordinary migratory behavior. Both young and old migrate south out of the Black Sea, and many of the younger individuals seem not to return. The older ones leave the Sea of Marmara in summer for the Black Sea without having spawned. The old homeland with its higher salt concentration is no longer the spawning place but merely a region into which a part of the Black Sea population wanders for the winter. The reason for this peculiar behavior is not known as yet.

Besides the tropical forms of Indian origin in the Anatolian fauna of freshwater fish, there is one other group of fishes which is completely lacking in Europe. For this the cyprinid genera *Acanthorutilus* (Anatolia and Mongolia), *Varicorhinus,* Anatolia, Transcaucasia, Syria, Palestine, Africa), *Acanthobrama* (western Anatolia to Palestine, its nearest relative *Capoëtobrama* in the Amu Daria and Syr Daria in central Asia), and *Schizo-*

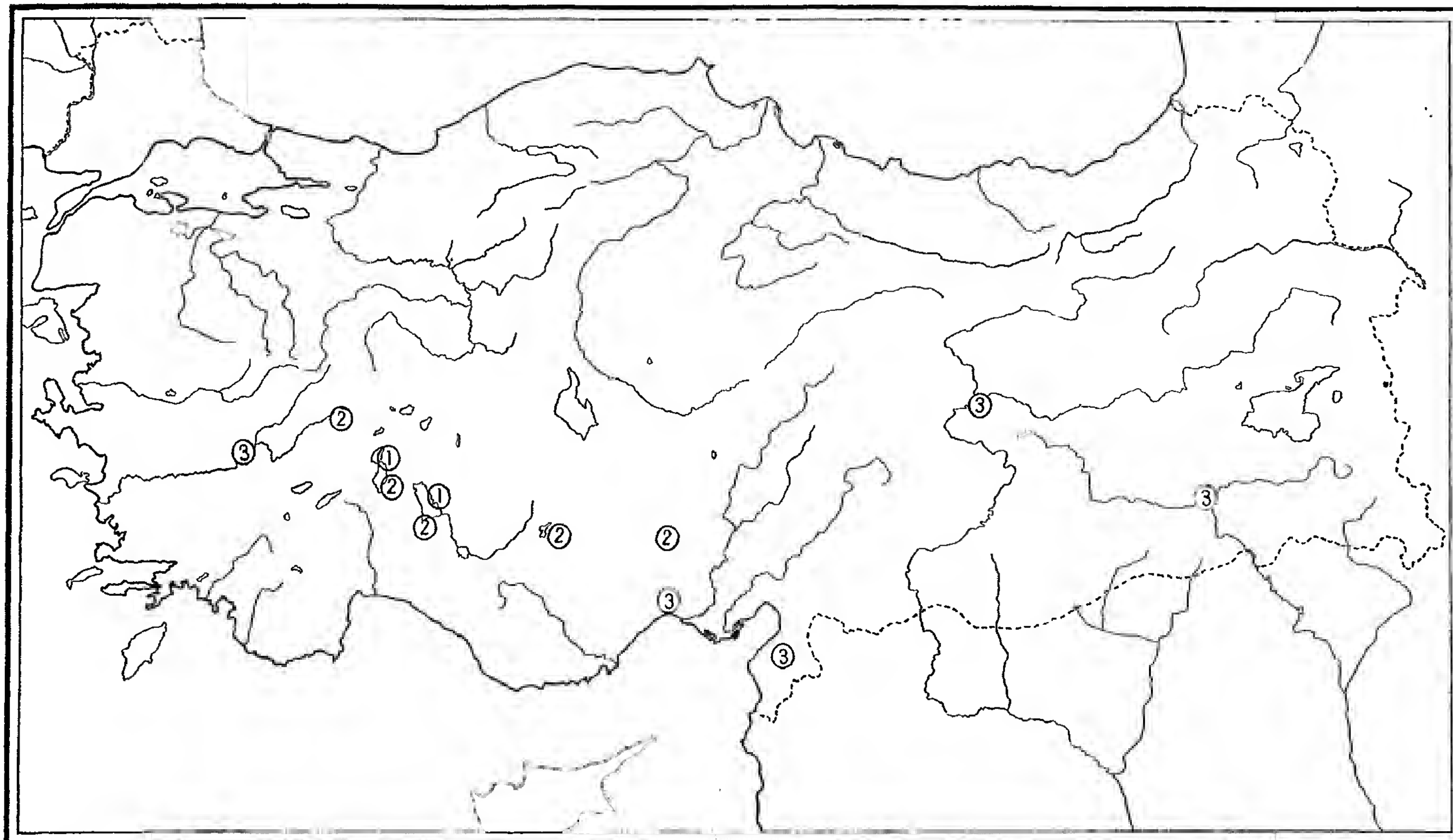


Fig. 10. Fishes of central Asiatic relationship in Anatolia. 1. *Schizothorax prophylax;* 2. *Acanthorutilus* (3 or more species); 3. *Acanthobrama* (3 species).

thorax (central Asia and as a glacial relic in India) can be named. The Bosphorus is, from the geological point of view, a very recent formation (Pfannenstiel, 1944); nevertheless it is an absolute barrier to the westerly distribution of all these Asiatic forms (Figs. 10, 11). The rich representation of some of these genera in Asia Minor and the distribution of some of their species over many river systems of Anatolia favor the assumption that the relative age of these forms is great. If this statement is correct, the original western frontier of all these species cannot have been the Bosphorus and the Aegean Sea, only formed, as seen above, during the Quaternary. It is more probable that these forms, which are richly represented in the mountainous regions of western and central Asia, entered Anatolia so early that they could make full use of the way southward into Palestine and even into Africa. This way is known as the Pliocene land-bridge in the Syrian-Iranian area. If this hypothesis is true, the Bosphorus and the Aegean Sea could not play the decisive role in the separation of these Asiatic genera from Europe. The frontier of these Asiatic elements in Anatolia was more likely the western Anatolian mountain system, by which the Aegean zone is separated from the plains of central Anatolia (Fig. 12). It is a well-known fact that the upper beds of the different rivers on the Aegean slope of the western Anatolian mountains have retained only secondary relationship with the central Anatolian high plateau and the remnants of the lake system which once covered it. The overground connection of these lakes is even now only partially extant; many lakes send their waters by underground passages through the mountains to the rivers on the Mediterranean or the Aegean slopes of southern and western Anatolia.

Similarly, in the south and in the north, high mountains separated the central Anatolian lake from the Mediterranean as well as from the Black Sea (i.e. the Sarmatian coast). From the east, on the other hand, the entrance into central Anatolia was more or less open and facilitated by the upper reaches of the eastern Anatolian rivers, which flow from east to west. The union of the Aegean coast with central Anatolia by the modern river systems was definitely effected after the Aegean continent broke down. As the Asiatic forms came too late, they found no freshwater routes by which to pass to the European side of the Aegean Sea.

Let us now return to the problems concerning the Anatolian steppes. As stated above, the altitude of Anatolia was reached only in the course of the second half of the Tertiary or even later. Salomon-Calvi (1939) dates the rise of Anatolia as late as in the Quaternary, supposing that the two phenomena, the Aegean subsidence and the elevation of Anatolia, were the expression of the same crustal movement in this region. The Tertiary climate in the interior of Anatolia was warmer and wetter than it is today. In the Quaternary the humidity increased. As a result, the surface of the lakes which have persisted to the present day as brackish water, like the lake of Burdur, at that time stood 90 metres higher (Louis, 1938). Remnants of old lake terraces with clearly visible traces of the eroding waves surround the Great Salt Lake; the lake of Van is only a small relic of a greater inland sea, covering not only the territory of the lake of Van but also that of the plains of Mush. The majority of the central Anatolian lakes were in connection with one another (Lahn, 1948). A rich vegetation surrounded this watered panorama of glacial Anatolia.

Recent research has shown that the natural lower boundary of forests of a more or less dry type lies so deep that even today the whole area from the west of Malatya to Bitlis must be included in the forest zone and does not belong to the steppe facies (Louis, 1939). Natural steppes are found in central Anatolia, in the high plateaux around Mount Ararat, and in the south of the eastern Toros, in

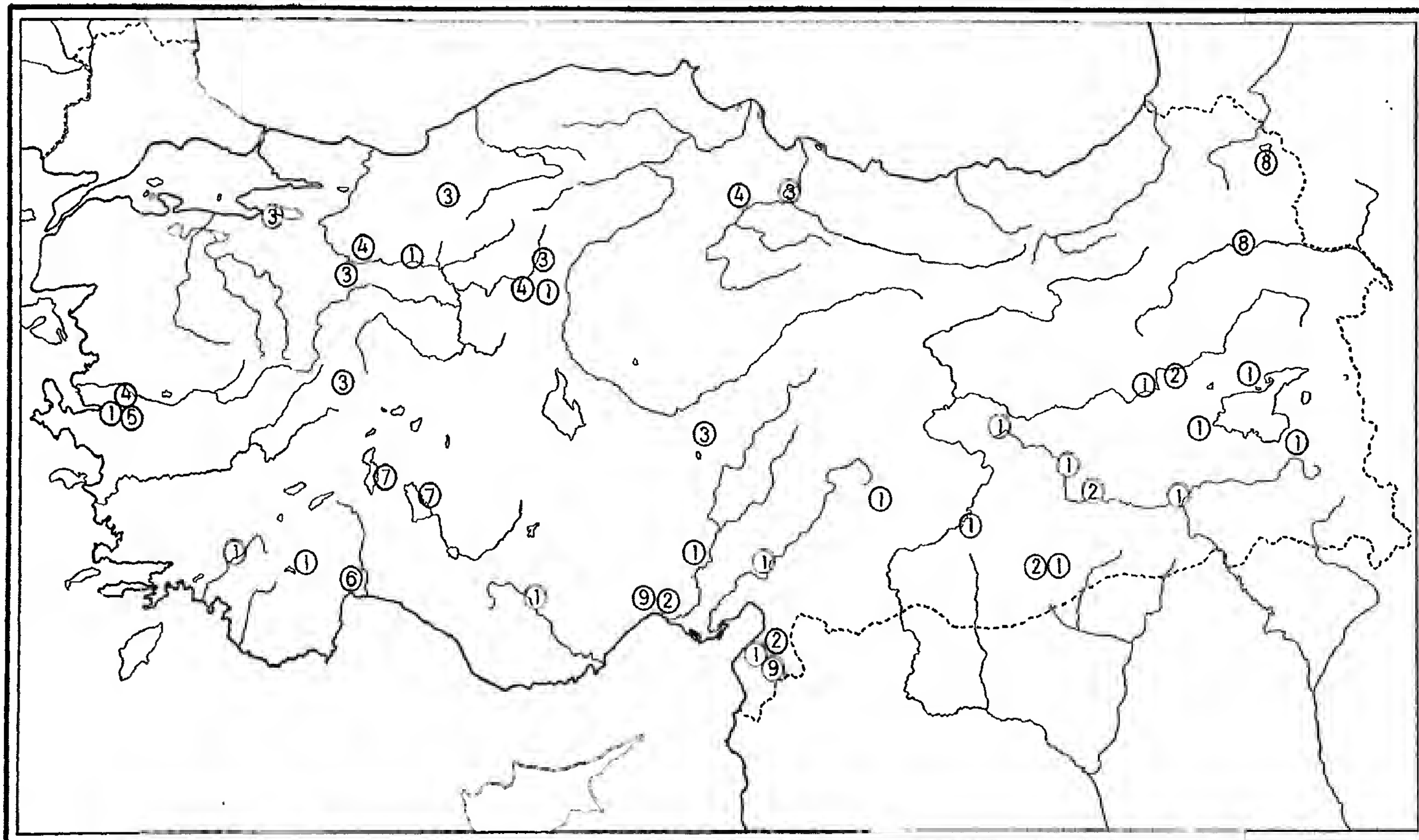


FIG. 11. The distribution of the genus *Varicorhinus* in Anatolia. 1. *V. damascinus;* 2. *V. trutta;* 3. *V. tinca;* 4. *V. sieboldi;* 5. *V. holmwoodi;* 6. *V. antalyensis;* 7. *V. pestai;* 8. *V. capoeta;* 9. *V. barroisi.*

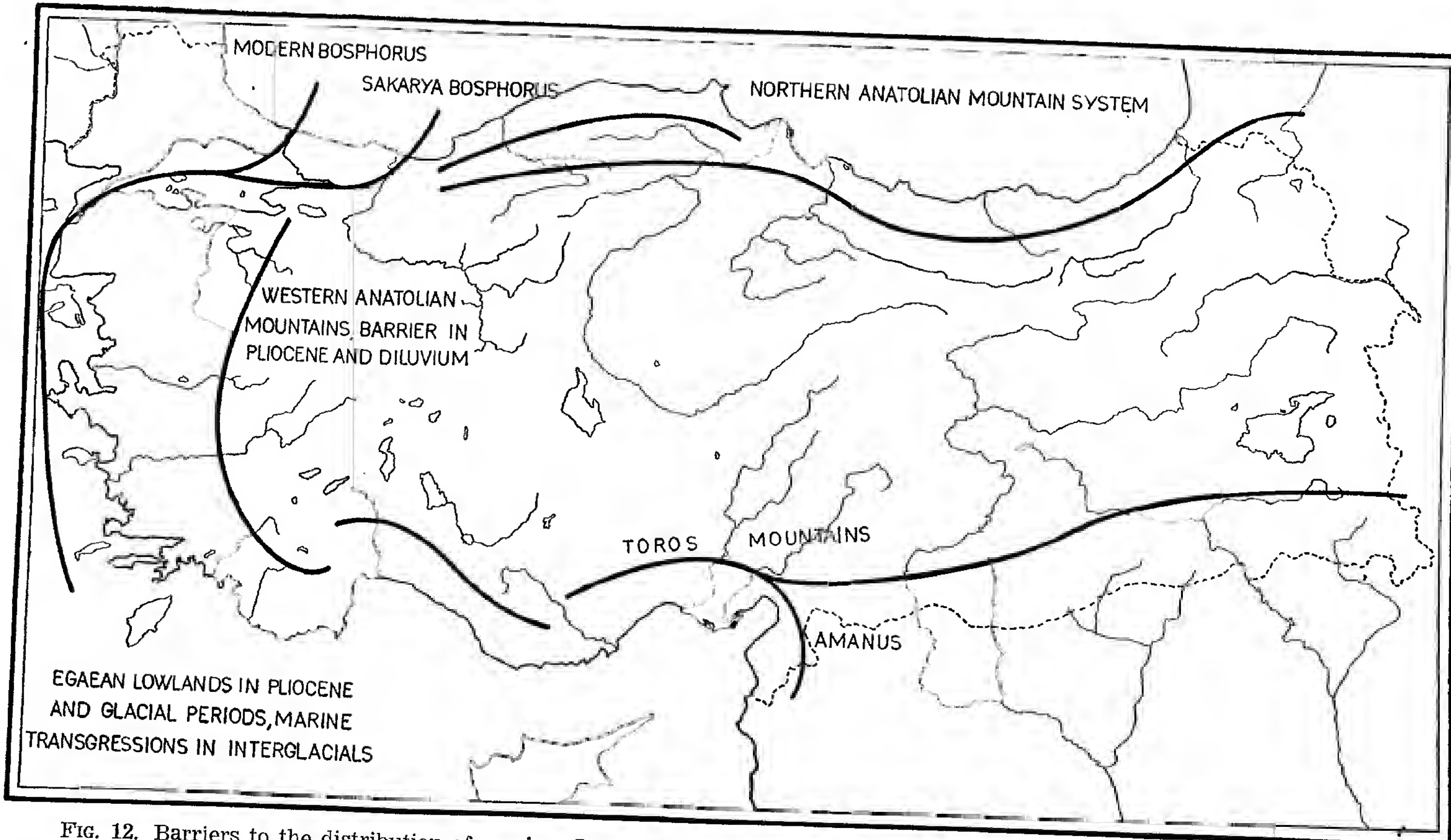


FIG. 12. Barriers to the distribution of species. In addition to the mountain systems in northern, southern, and western Anatolia, the Aegean lowlands acted as a faunistic barrier, either as a system of fresh or brackish water in glacial periods and in the Pliocene, or as the result of a marine transgression. Before the functioning of the modern Bosphorus there was a communication in interglacial periods between the Black Sea and the Mediterranean through the Sakarya Bosphorus of Pfannenstiel.

the area which forms the continuation of the warmer Syrian steppes towards the north. The fauna of these Eremial regions is derived to a great extent from forms which in earlier times inhabited the Arboreal, but still exist in the same regions which underwent steppification later. The Anatolian butterflies and moths, for example, have systematic relationship mostly with the central European and Mediterranean fauna, but not with that of central Asia, where, for a very long period, the Eremial facies has been characteristic. Among the mammals of Anatolia, especially in the rodents, the percentage of steppicolous species is greater than in most other orders. *Spalax, Spermophilus, Alactaga, Cricetulus* may be mentioned here. In the Reptilia the number of typical Eremial genera is high only in the eastern steppe zone, i.e., the Ararat plateau. Here *Phrynocephalus, Eremias,* and *Eumeces* represent the real Eremial fauna. Only one species, *Eumeces schneideri,* has been found once in the well-investigated central steppes near Ankara. In this latter region, besides the euryoecious *Ophiops elegans,* a species of *Lacerta, Lacerta parva,* derived from the Arboreal, has adapted itself to the conditions of life in the steppe. The same is true for the remarkable, rare, and primitive *Lacerta princeps* in the southern Anatolian steppes (Mertens, 1952). (Fig. 13.)

The Marine Fauna

Even in a short review of only some of the problems of historical zoogeography in the Near East, the marine fauna with its changing scenery cannot be neglected. In the beginning of the Tertiary, the Tethys Sea covered large areas which today are dry land. From the West Indies to the Pacific Ocean a rich community of tropical animals populated the littoral zone of this sea, surrounded by coral reefs. In the second half of the Tertiary great changes occurred in that part of the Tethys which was finally to be transformed into the Mediterranean of today. Landbridges rose, cutting off the continuity of the sea. The loss of communication with the Indo-Pacific has lasted to the present. The rich fossil-bearing beds of Lebanon and of Monte Bolca in Italy give us information about the great number of tropical genera in the Mediterranean of that time, while now they are confined to the Indian and Pacific Oceans. Ekman (1935) found general agreement for his thesis that the extinction of the tropical fauna of the Tethys in the Mediterranean was the result of the fall in temperature in late Tertiary and Quaternary times.

In the modern fauna of the Mediterranean, again, tropical forms play the decisive role, but these forms are related mainly to the fauna of the warmer parts of the Atlantic Ocean. Besides these, species with boreal relationship can also be found. It is probable that they entered the Mediterranean in the recent past, when, as a result of the cooling of the Atlantic to lower latitudes, the boreal area extended further to the south. Some of the boreal invaders of that time persisted in the Mediterranean into the postglacial period, mixing with aggressive and euryoecious species of tropical and subtropical distribution in the Atlantic. It is still not known definitely whether the majority of these species persisted in the Mediterranean itself during the period of its separation into different parts and its cooling or—as is more probable—whether they later reoccupied this sea. The ecological efficiency of these species is clearly demonstrated by the fact that they freely entered the much colder Black Sea, definitely establishing themselves there. As a result of the rhythmic transgressions of warmer Atlantic waters to the north, truly equatorial species of this ocean appear from time to time on the English coast and more frequently in the Mediterranean, especially in its western parts and on the Algerian coast. But such forms apparently are not sufficiently adapted to the conditions in the Mediterranean. Some which persisted remain

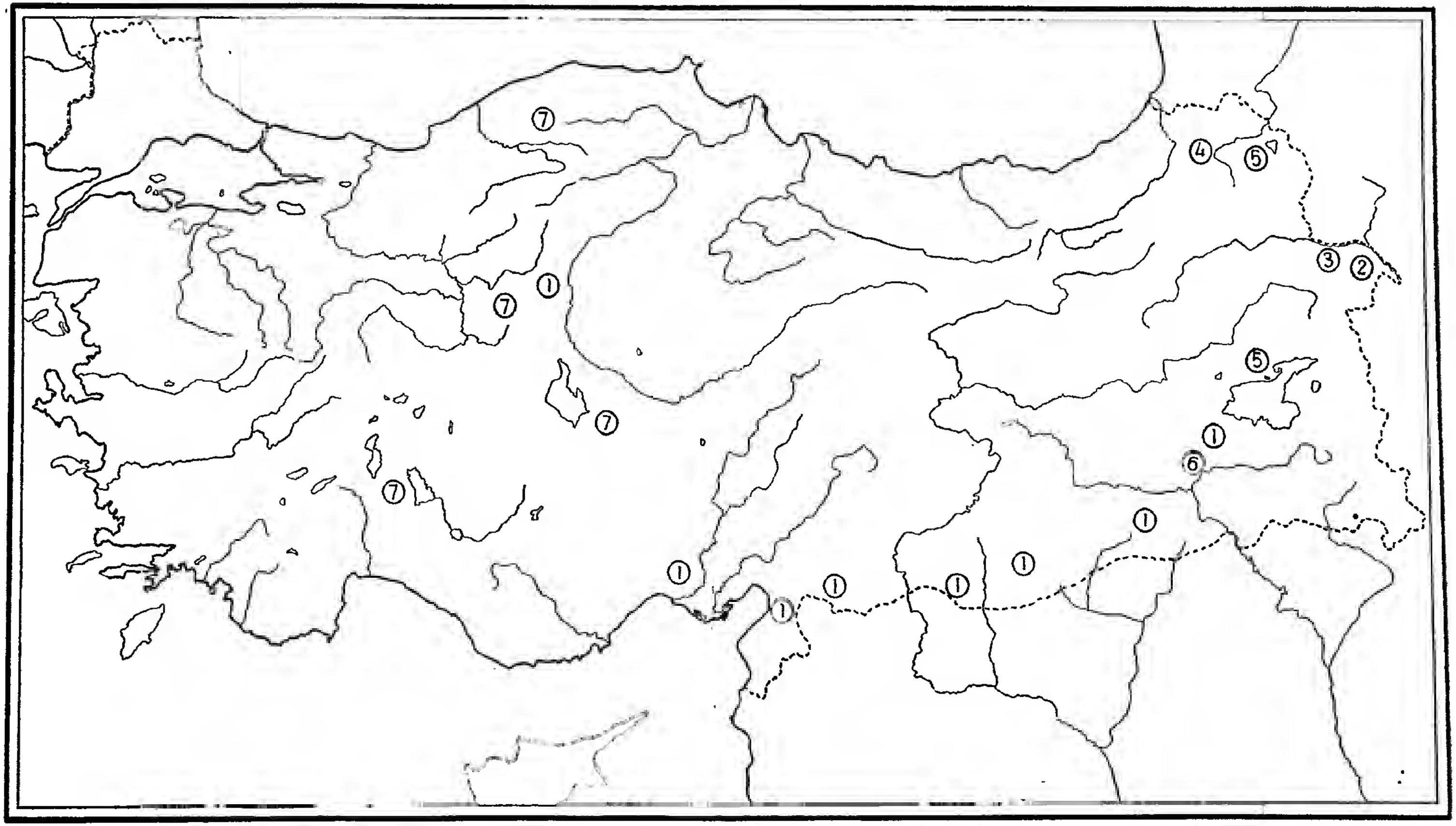


FIG. 13. Steppicolous lizards of Anatolia. 1. *Eumeces schneideri* (2 races); 2. *Phrynocephalus helioscopus persicus;* 3. *Eremias pleskei;* 4. *Eremias arguta;* 5. *Eremias velox strauchi;* 6. *Lacerta princeps;* 7. *Lacerta parva.*

rare, others died out after short periods, e.g. *Diodon hystrix*.

It is not certain whether for this phenomenon physical or biological conditions are decisive. For instance, the prior occupation of all ecological niches by well-adapted species could have prevented the successful establishment of these late invaders from the equatorial regions of the Atlantic. Information, for which we are indebted to W. Steinitz (1927, 1929), is sufficient to contradict this view. Since the opening of the Suez Canal in 1869 an invasion of the Mediterranean by species of the Indo-West Pacific fauna has begun. These species coming from the Red Sea, the warmest and saltiest sea we know, have passed through the Suez Canal with its changing and extreme ecological conditions, probably in the course of some generations, and safely reached the Mediterranean. Ten species, which have expanded into the eastern Mediterranean by the aid of the northward current, were recorded by W. Steinitz from Haifa in 1927. Another ten were added to this list twenty years later by G. Haas and H. Steinitz (1947). Ben-Tuvia (1953) described the presence of eight other species which arrived in the Mediterranean off the coast of Israel. Ten species at least, partly different from those known from Haifa, can be found in Alexandretta (Kosswig, 1950); four of them are known from Rhodes at the entrance to the Aegean Sea, since 1943. All these facts indicate that these tropical Indo-Pacific forms, with very different biological requirements, have found a great variety of suitable ecological niches. The degree of plasticity which these Erythraean fish, Crustacea, bivalves and others show, is remarkable and not in harmony with Ekman's supposition that the ancestors of these new invaders died out in the Mediterranean at the end of the Tertiary as a result of the cessation of the limited environment in a tropical coral sea.

The animals of the tropical Tethys Sea had millions of years at their disposal for their adaptation to the cooling of the climate in the Tertiary. We must conclude that at least conditions such as those prevailing today in the southern Aegean Sea are well within the range of tolerance of those Erythraean animals which at present are flourishing there and expanding their area of distribution, e.g. the fishes *Mulloidichthys auriflamma* and *Siganus rivuletus* and the crab *Portunus pelagicus* (Fig. 14). It therefore seems more probable that the dying out of the tropical Tethys fauna is merely the result of either a further lowering of temperature or a change in salinity in the Mediterranean during the glacial periods when Arctic species (*Cyprina islandica, Plautus impennis*) lived in that sea.

This invasion of Erythraean species into the Mediterranean is the more remarkable as reverse infiltration of Mediterranean forms into the Red Sea has been very limited (Gohar, 1954). Among the fishes of economic importance, only *Serranus cabrilla* and *Sciaena aquila* may be mentioned; these are frequently caught in the Red Sea as far as 90 km. to the south of Suez. Although the Red Sea itself represents a relatively young geological structure, it seems that at the moment of its formation species adapted to all ecological niches were waiting *ante portas* to enter this sea. In the Mediterranean the situation is quite different. It is possible that there are, even now, free ecological niches in the eastern Mediterranean although approximately 80,000 years have passed since the last culmination of the glacial period (Würm I), and some 18,000 years have passed since the last, but less important, glaciation (Würm III). Or it may be that the Atlantic species, the older inhabitants of the eastern Mediterranean, are less adapted to the conditions in this sea than are the newcomers from the south.

These invasion phenomena correspond in an interesting way to the ingress of Mediterranean species into the Black Sea at the end of the glacial period, also against a gradient of temperature and salinity. Here zoogeographical phenom-

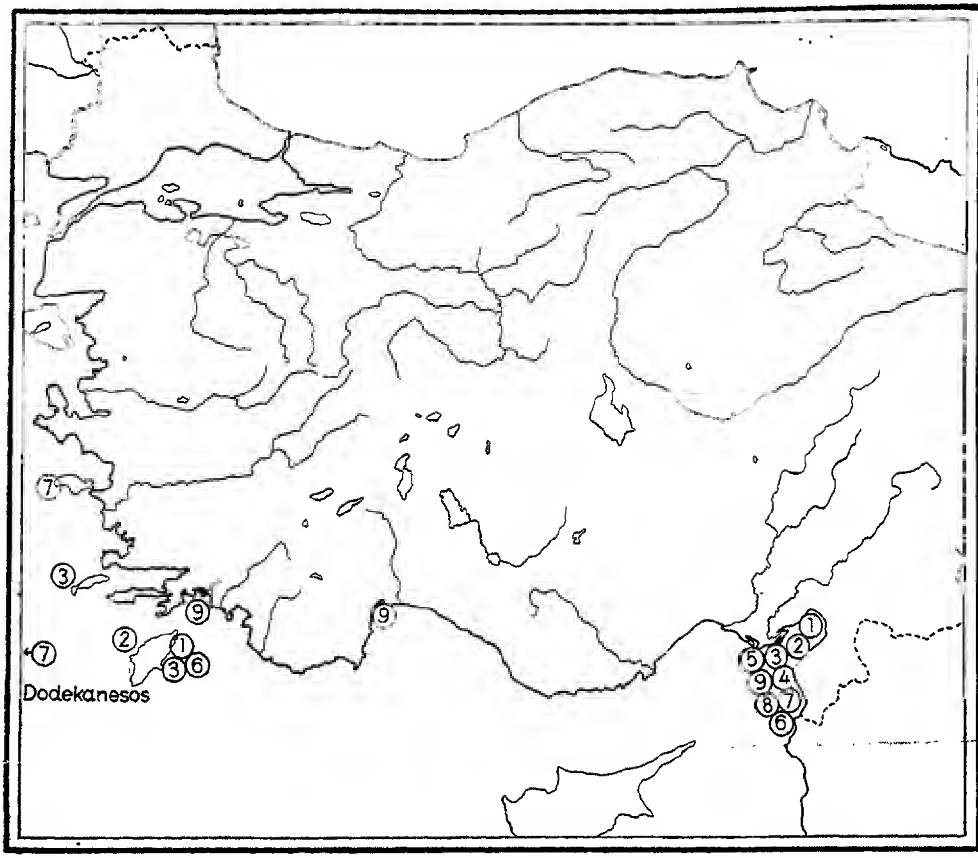


FIG. 14. Erythraean species off the Anatolian coast. Fishes: 1. *Stephanolepis ocheticus;* 2. *Mulloidichthys auriflamma;* 3. *Siganus rivulatus;* 4. *Atherina pinguis;* 5. *Leiognathus klunzingeri;* 6. *Holocentrum rubrum;* 7. *Tetraodon spadiceus;* 8. *Upeneus* cf. *tragula.* Crustacea: 9. *Portunus pelagicus.*

ena touch on problems of genetics and evolution, the discussion of which is outside the scope of this paper. It may be sufficient to consider briefly the results of the greatest biological experiment man has ever undertaken, albeit unwittingly: the opening of the Suez Canal. The ensuing ingress of species from the Red Sea into the Mediterranean cannot be understood as adaptation resulting from slow and stepwise genetic changes, but only as the sudden manifestation of ecological potentialities which for many generations had never been tried and which could never have been of functional significance. The same may be true for the occupation of the Black Sea by warmth-loving newcomers from the postglacial Mediterranean, when communication between the two seas was established by enormous geological changes which occurred in a relatively very short period of time.

As stated above, it is not clear to what degree modern Mediterranean species have persisted in that sea in the second half of the Tertiary and in the Quaternary. The temperature underwent extensive fluctuations, allowing the invasion of boreal and Arctic forms at one extreme and of tropical species such as *Strombus bubonius* and *Purpura haemo-*

stoma at the other. The sea level also fluctuated during the glacial periods, being lowest during the glaciation when large quantities of water were bound as ice near the poles. The Mediterranean at such times of lowest level was transformed into an inland sea and partially, if not completely, divided into two parts by the exposed land connection between Sicily and North Africa. H. Steinitz (1949) is inclined to suppose that the modern Mediterranean blennies are relics *in loco* of the Tethys in our region. But it must be kept in mind that, like most marine animals, blennies have pelagic larvae, which by passive locomotion could re-occupy an area lost in the past.

On the other hand there are, in fact, relics of the old fauna of the Tethys even in places where they would be least expected to survive: in fresh and brackish waters of the Anatolian plateau, as well as in similar biotopes in the regions around the Mediterranean which are nearly at sea level. I should like to draw attention to a family of small fish, the cyprinodontids. The genera *Cyprinodon* and *Aphanius* consist of some species in central and southern North America, and others around the Mediterranean and in central Anatolia, in the Dead Sea region, and finally in the western part of the Indian Ocean, including the Red Sea. Apparently this distribution as a whole corresponds to the western part of the Tethys. Everywhere these small fish live in such biotopes as marine coastal waters, the mouths of rivers, in lakes in the neighborhood of the sea, in fresh and salt springs inland, swimming freely in waters of very different salt concentration. As stated above, Anatolia, nearly at sea level in earlier geological periods, was elevated later. Cyprinodontids, having migrated inland, were thrust up with the rising Anatolian land mass. Because of their euryhalinity, they were able to survive in many places and today form one of the most characteristic groups in Anatolia and also in Palestine. It may be added that the enormous degree of variability with which we are confronted in the Anatolian cyprinodontids seems to be caused by interspecific or even intergeneric crosses in the past (Aksiray, 1952). Many of the populations of these fishes which at first sight look like different species, subspecies, or even genera are in reality, as it seems, nothing other than groups of a large hybrid swarm which in isolated populations have attained a more or less clear degree of uniformity; other populations are still heterozygous and composed of many different phenotypes.

It is probable that other survivors (Kosswig, 1943; Lohmander, 1939) of the Tethys are to be found among some of the subterranean genera of invertebrates around the Mediterranean and in Central America, including relatives of many marine forms of today. Such genera as *Caecosphaeroma, Monolistra,* and others may be mentioned. The transition of the ancestors of these cavernicolous forms to life in darkness was most probably accomplished by adaptation to specialized conditions of life in dark, cave-like places in the sea. Later, by the elevation of such formations rich in limestone, these forms became members of the subterranean inland fauna, without having passed through a stage of phylogenetic development in the superficial freshwaters of the continents.

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CURT KOSSWIG, now Professor of Zoology at the Zoological Institute, Hamburg, Germany, was Professor of Zoology at the University of Istanbul, Turkey, when this paper was written.

The author adds: "The results presented above are, to a great extent, based upon new records obtained in the course of many excursions into different regions of Anatolia during 17 years. The material help liberally granted by the Rectorate of the University of Istanbul and the Decanate of the Faculty of Science facilitated these scientific trips. In the course of our travels we found the local State authorities of the greatest understanding and readiness to help whenever required. I wish to ~~express to them our~~ gratitude in the name also of my collaborators who participated in these excursions. Wherever we came we were deeply impressed by the generous hospitality with which we were honoured even in the most remote villages of the country. Our task could not have been completed without the sincere interest shown by many private people all over Anatolia."